THE INFLUENCE OF GROWTH STAGE AND APPLICATION SITE ON MOVEMENT AND EFFECT OF GLYPHOSATE IN *CIRSIUM ARVENSE* (L) SCOP.

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ABSTRACT

Glyphosate was applied at different rates to the upper parts of Cirsium arvense plants at various growth stages in a glasshouse experiment. Measurements and observations were made of the plants over a period of several months following treatment. In other experiments, glyphosate was applied to different parts of plants and to either side of leaves to determine the importance of herbicide placement on its subsequent effectiveness.

Complete death of plants, as signified by decomposition of the roots, generally occurred only where the maximum dose (100 mg ai/plant) was applied, and occurred consistently only for those plants treated at the post-flowering growth stage. However, plants treated on the lower parts of stems died in some cases after application of 25 mg.

The symptoms and damage resulting from glyphosate action are described and discussed. Extensive translocation of glyphosate appeared to occur, both symplastically and apoplastically, with greater translocation to the roots and untreated daughter stems occurring from treated tissue situated low on the stem. Stem tissue seemed as efficient at absorbing glyphosate as leaves, and likewise no difference in absorption rates by upper compared with lower leaf surfaces was detected.

Complete control of plants occurred only if all stems simultaneously wilted approximately 1 month after treatment, apparently due to disruption of the roots.

Plants varied considerably in response to treatment and no relationship could be established between degree of effect and plant size, plant sex or relative humidity at the time of treatment.

The results are discussed in relation to ropewick application of glyphosate to C. arvense plants.

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LIST OF PESTICIDES

The chemical names of pesticides appearing in this text are listed below:

acephate	OS-dimethyl acetylphosphoramidothioate
amitrole	3-amino-1,2,4-triazole
barban	4-chlorobut-2-ynyl N-(3-chlorophenyl)carbamate
bromoxynil	3,5-dibromo-4-hydroxybenzonitrile
2,4-D	2,4-dichlorophenoxyacetic acid
dalapon	2,2-dichloropropionic acid
dicamba	3,6-dichloro-2-methoxybenzoic acid
dichlorvos	2,2-dichlorovinyl dimethyl phosphate
glyphosate	N-(phosphonomethyl)glycine
maleic hydrazide	1,2,3,6-tetrahydro-3,6-dioxopyridazine
MCPA	4-chloro-2-methylphenoxyacetic acid
picloram	4-amino-3,5,6-trichloropicolinic acid
terbutryne	6-t-butylamino-4-ethylamino-2-methylthio-1,3 5-s-triazine
zineb	zinc ethylene-1,2-bisdithiocarbamate

INTRODUCTION

(1) CIRSIUM ARVENSE:

Cirsium arvense (L.) Scop. is an aggressive perennial weed found in many parts of the world. It is a native of Europe or temperate Asia (Holm et al 1977) and, although called Californian thistle in New Zealand, is known also as creeping thistle or Canada thistle in other countries. C. arvense is distinguished from other thistles by its perennial branching roots; its dioecism; its small, almost spineless heads; and by its characteristic of growing in circular patches, with each new patch usually consisting of only one clone (Holm et al 1977). The stems grow erect to a height of 40 to 120 cm, arising from numerous points on the horizontal roots. The leaves are usually dark green, deeply lobed, and ruffled on the margin, with spines around the margin and at the tip of the lobes. Flowers are borne at the apex of stems. These stems are terminal or arise from leaf axils and branch several times. The flowers are mostly purple or blue with various shades; occasionally they are white (Hodgson 1968).

(a) Shoot Development:

Stems can develop from seeds or from root systems. Seedlings usually develop slowly and are quite sensitive to competition from other plants (Bakker 1960; Amor and Harris 1975). Stems developing from roots or stem fragments are less sensitive and can penetrate dense pasture swards, although subsequent growth may be retarded if the pasture plants are strongly competitive (Holm et al 1977).

C. arvense plants emerge mainly in spring and form rosettes. Hodgson (1964) found they generally begin vertical shoot growth about three weeks after emergence, and this stops about two months later, at which time the stems flower and produce seed. The stems die back in autumn, and the plant overwinters as a series of root segments (Sagar and Rawson 1964).

(b) Root System:

C. arvense spreads in the soil by means of both roots and rhizomes. The development of the root system has been described by Hayden (1934), Bakker (1960), and Sagar and Rawson (1964). Seedlings first develop a

taproot with numerous fibrous secondary roots. The taproot soon thickens as assimilates accumulate and, under favourable conditions, lateral running roots are produced by the taproot 6-8 weeks after germination. After growing horizontally for 6-12 cm, these running roots bend downwards and at the point of bending a new horizontal root usually develops and continues the horizontal spreading. Sections of these running roots thicken and develop vertical rhizomes which grow to the soil surface and form new stems. The thickening of the root results from the production of storage parenchyma within the stele, and by the end of the growing season, such roots may be up to 1.5 cm in diameter. Assimilates produced by the stem are stored in this parenchyma tissue. Other stems can develop from the underground sections of these stems or from the original taproot. Thin lateral roots and adventitious roots arise respectively from the horizontal running roots and underground parts of the aerial shoots, and their function is the uptake of water and nutrients.

Roots are usually found at a depth of 1-75 cm below the soil surface, though this depends on soil properties (Arnold 1980), and roots have been found at depths of 6 m (Holm et al 1977). Stems can develop from root systems at depths of 90 cm (Friesen 1968), though most stems develop from roots in the upper 30 cm of the soil (Hayden 1934). Hamdoun (1972) found that fewer stems were produced from root fragments as their depth of burial increased from 10 to 50 cm.

A single plant can spread rapidly, and Hamdoun (1967) reported that 1-year-old plants may expand and produce enough shoots to occupy an area almost 2 m in diameter with roots extending down 70 cm. The running, horizontal roots die off a little from the end of origin each season while the tip continues to grow as new plants are formed (Amor and Harris 1975).

Hayden (1934) states that vertical shoots or rhizomes are able to produce roots and buds at all nodes, should they be broken up, whereas horizontal and vertical roots may produce buds and roots at any point. Root segments need to be at least 5 mm long to give rise to stem buds though, and more vigorous growth occurs from longer segments as these have more reserves (Hamdoun 1972). Plants generally emerge from root and stem pieces in about 15 days (Prentiss 1889). However, roots have a period of dormancy coincident with the onset of short days, reduced

temperatures, and senescence of top-growth (Henson 1969).

(c) Flowers and Seeds:

C. arvense flowers are borne on separate male and female plants, though Lloyd and Myall (1976) report that dioecy is not absolute as some males produce occasional fruits. The plants require a photoperiod of at least 16 hours to ensure flowering (Link and Kommendahl 1958). Bakker (1960) claims no flowers are produced by the first aerial shoots to develop from seed in the field, but all mother stems did flower in the present glasshouse experiments. The flowers are insect-pollinated (Dersheid and Shultz 1960). Hay (1937) reports that one flowering stalk may produce up to 5300 achenes, but the average production is 1530.

The achenes of C. arvense develop a pappus, though Bakker (1960) considers the seeds are not dispersed as far as is popularly imagined because the pappus tends to separate from the achene, leaving the achene in the flower-head. Holm et al (1977) postulate that seed dispersal is by most of the conventional means available to weed seeds, such as by water, dirty crop seeds and farm machinery. The seeds germinate well (Hodgson 1968).

(d) Distribution:

C. arvense is reported as a weed of 27 crops in 37 countries, and is confined to countries with a temperate climate: it is rarely seen as a weed near the equator (Holm et al 1977). In New Zealand, it has limited distribution in Northland (Matthews 1975), and although it is well distributed throughout the rest of the country, is most abundant in coastal Southland and some elevated regions, eg about Raetihi (Taylor 1980).

Holm et al (1977) report that the species is adapted to areas of moderate rainfall and summer temperatures. Many of the serious weed problems are in areas receiving 450 to 900 mm of rainfall per year. A high water table severely limits root growth. The plant can survive on a wide range of soil types and will tolerate a 2% salt content, though it is less common or often absent from very light, dry soils. It is most competitive on deep, productive, well-aerated soils which do not become too warm.

(e) Significance as a Weed:

(i) Effects:

When established, C. arvense competes strongly with crop plants for light, moisture and nutrients (Moore 1975). Yield reductions in wheat (Triticum spp) of 60% have been measured by Hodgson (1968) with thistle densities of 25 shoots/sq m. Other crops in which C. arvense is a troublesome weed include barley (Hordeum vulgare), flax (Linum usitatissimum), millet (Panicum miliaceum), oats (Avena sativa), rye (Secale cereale), sorghum (Sorghum bicolor), beans (Vicia faba), peas (Pisum sativa), maize (Zea mays) and rape (Brassica napus), as well as in orchards, vineyards and pastures (Holm et al 1977).

In pastures, this weed creates the additional problem of reducing pasture utilization by stock because of its prickly nature. Hartley and James (1979) found that sheep grazed in thistle-free pastures had liveweight gains up to 40% greater than sheep in pastures infested with C. arvense.

Apart from the effects of competition and reduced pasture utilization, C. arvense has been shown to produce allelopathic substances which could affect the successful establishment of such crops as barley, ryegrass (Lolium spp) and clover (Trifolium spp) (Bendall 1975), although the importance of this phenomenon needs further investigation.

(ii) Causes:

There are several reasons why C. arvense is a persistent weed problem. Its ability to produce vigorous regrowth from its root system means control measures must be aimed at the underground parts of the plant. Techniques which involve killing only the above-ground parts, such as mowing or using non-translocating herbicides, are of little use unless they are repeated frequently to deplete the carbohydrate root reserves (Ivens 1978). A number of translocated herbicides are available which can move into the C. arvense roots and give good control. Picloram and glyphosate are particularly suitable for this purpose (Kirkland 1980). However, the effectiveness of any particular control measure can vary considerably with C. arvense, and the reasons for this are often not understood.

One factor which determines effectiveness is the growth stage at which the plant is treated (Marriage 1980). The level of carbohydrates stored within the roots and the direction of translocation both vary with growth stage and can influence control effectiveness. This will be covered in more detail in the next chapter.

Hodgson (1964) found considerable variation in the morphology, physiology and phenology of ten C. arvense ecotypes grown under the same conditions. This genetic variability also involves susceptibility to control measures, and various workers have found some ecotypes more susceptible than others in their response to cultivation, 2,4-D, amitrole, dicamba, picloram and glyphosate (Hodgson 1970; Hunter and Smith 1972; Saidak and Marriage 1976).

One major reason why C. arvense remains a troublesome weed in many situations is that the herbicides which can give good control of this plant are non-selective and so cannot be used without unacceptable levels of damage to surrounding crops and pasture. This problem tends to be greater in the latter case though as non-selective weed control is often possible between the harvest of one crop and establishment of the next.

(2) ROPEWICK APPLICATORS:

A number of herbicide application techniques have been devised to selectively treat weeds which grow taller than the surrounding crop. The recirculating sprayer uses the principle of spraying solid streams of herbicide horizontally above the level of the crop into a trap, from where it is returned to the original spray tank (McWhorter 1970). Weeds growing above crop level intercept this herbicide while the crop plants remain unharmed. The recirculating sprayer was developed in the 1950s to control Rumex obtusifolius in New Zealand pastures using 2,4-D (Edmond 1955), but it found only moderate utilization until the introduction of the non-selective, translocated herbicide glyphosate in the 1970s (Schneider et al 1982).

Herbicide from recirculating sprayers can cause crop damage due to splashing and spray drift. Applicators have since been introduced which make use of the height differential between crop and weeds by wiping

herbicide on to the weeds, thereby further reducing the risk of crop damage (Fawcett and Becker 1979).

One such applicator is the roller applicator, which was developed and first used for perennial grass control in Poa pratensis seed-production fields in Minnesota, USA (Wyse and Habstritt 1977). In this applicator herbicide is dispensed onto a carpet-covered cylinder, which rotates and wipes the underside of leaves and stems of tall-growing weeds as the machine travels through the crop (Schneider et al 1982). Maintaining the desired saturation of herbicide solution in the carpet to give proper weed control, yet eliminate excess dripping, presented a problem (Irons and Burnside 1978), which has been overcome by installing a moisture sensor that activates a solenoid as the carpet moisture content drops (Schepers and Burnside 1979).

The most widely used herbicide-wiping device at present is the ropewick applicator, designed by Dale (1978). It consists of a herbicide-filled polyvinylchloride pipe, 8-10 cm in diameter, which is sealed at either end. A series of braided rope (1.3 cm diam.) segments 45 cm in length are positioned along the front of this pipe so that the mid 20 cm portion is exposed on the exterior surface while each end bathes in the herbicide solution within the pipe. Rubber grommets seal the pipe where ropes are inserted. The pipe is mounted on a tractor and, while being pushed through tall weeds, herbicide moves through the rope by capillary action and is wiped onto the weeds. Two rows of overlapping rope segments are used so no weeds are missed.

As well as making it possible to use non-selective herbicides in some crops, these applicators use herbicide more efficiently than conventional spraying equipment. In theory, the only herbicide left in the field is that applied to the weeds, thereby eliminating wastage, minimising the possibility of environmental contamination, cutting down the volume of herbicide to be transported about the farm, and considerably reducing the cost of treatment (Costa 1981). Because of its simplicity, the ropewick applicator has the added benefits of being cheap and easy to use (Dale 1979).

Since its development, the ropewick applicator has been used to apply glyphosate to a number of troublesome weed species, and good control has been obtained with Juncus spp, Pteridium aquilinum regrowth (Campbell et

al 1981a); Rumex obtusifolius, Cyperus rotundus, Convulvulus arvensis, Phragmites communis, Allium oleraceum (Costa 1981); Sorghum halepense, volunteer maize (Zea mays) (Dale 1981); volunteer potatoes (Solanum tuberosum), sugar beet (Beta vulgaris) bolters, Asclepius syriaca, Cirsium arvense (Lutman 1980); Senecio jacobaea (Makepeace and Thompson 1982); Apocynum syriaca (Fawcett and Becker 1979); and Amaranthus hybridus (Long et al 1979).

However, the simplicity of the ropewick applicator has caused some problems. The movement of herbicide into the exposed wick is entirely by capillarity, and so the problem mentioned earlier with the roller applicator of keeping the wiper sufficiently moist to treat weeds adequately without allowing dripping also occurs in the ropewick applicator. Lueschen et al (1980) have found that a 33% concentration of glyphosate in water gives the optimum wicking rate. Higher concentrations seep too slowly and lower concentrations too quickly. This is the concentration recommended by Monsanto (1982). However, the ground speed of the ropewick applicator has to be reduced when treating dense patches of weeds so that the wick will remain sufficiently moist, and more than one pass over such weeds is often necessary to obtain satisfactory results (Derting 1980). Binning and Dana (1979) have found that roller applicators give better control in dense weed stands than ropewick applicators.

Research into the operation of ropewick applicators has indicated more efficient ways of utilizing the ropewick concept, and further improvements are likely. Derting (1980) found that better control was obtained when the wicks were positioned on the underside of the boom rather than on the forward-facing side, when the pipe reservoir was vented rather than closed, and when the rope segments were shorter. Lueschen et al (1980) investigated the effect on wicking rates of pre-soaking the rope, end-treatment of rope, method of installation, size of hole, nature of grommets, and the presence or absence of a sealing medium. Humburg et al (1981) found that the addition of a non-ionic wetter increased the flow rate of herbicides through the wicks. Makepeace and Thompson (1982) have shown that some rope types give better flow rates than others. Dale (1979) has noted that the use of ropewick applicators on hillsides can result in dripping from the lower end of the boom and drying of the wicks at the upper end. He suggests that the boom be constructed of shorter segments for such

situations, and Monsanto (1982) recommend travelling up and down slopes rather than across them.

Many of the drawbacks of the earlier applicators may have been overcome with the advent of the "Vicon Wedge-wik", a more sophisticated version of the ropewick applicator, its major advantage being the pressurised flow control of herbicide to the wicks (Vicon 1981). The pressure, and thus the flow rate, can be controlled by the operator to adjust for weed density.

(3) CIRSIUM ARVENSE, GLYPHOSATE AND ROPEWICK APPLICATORS:

(a) Present Situation:

There has recently been considerable interest in New Zealand in using glyphosate applied by ropewick applicator for controlling C. arvense. Glyphosate has given impressive results in the control of a number of problem weeds, especially Agropyron repens (Casely 1972), because of its very good translocation. It can give good control of C. arvense (Davison 1972) but its lack of selectivity makes overall application impossible in pastures and many cropping situations. The introduction of the ropewick applicator offered the possibility of selective application and raised hopes of obtaining greatly improved C. arvense control using glyphosate. However, field trials in New Zealand have resulted in only 40-80% control (R.W. Moore, pers. comm.) and the reasons for these relatively low kills are poorly understood.

Most work so far on the efficiency of ropewick applicators has been of an observational nature and such studies would be assisted by the development of a technique to measure accurately the amount of herbicide deposited on plants. In addition information is needed on the amount of glyphosate which has to be deposited on a plant to cause death.

Controversy still surrounds the question of which growth stage of C. arvense is most susceptible to glyphosate, and it is possible that translocation of herbicide deposited at the shoot tip by a ropewick applicator may have different characteristics from that following overall spraying. Whether the high concentrations of glyphosate used in ropewick applicators influence translocation also needs investigation, and the extent to which translocation is affected by the plant damage

resulting from the passage of tractor and wickboom is unknown. Similarly, very little is known about translocation from treated stems into neighbouring stems too short to be hit by the applicator. Likewise, no information is available on the amount of translocation into smaller, untreated stems needed to achieve effective control.

Environmental conditions are known to affect absorption and translocation of glyphosate by C. arvense (Gottrup et al 1976), but not enough is known for it to be possible to make firm recommendations about the best time for treatment.

(b) Objectives of this Work:

The present experiments were conducted to obtain information on those interactions between glyphosate and C. arvense of relevance to the performance of ropewick applicators. They were carried out in the artificial environment of a glasshouse, and the experimental technique used did not measure absolute glyphosate concentrations within plant tissue. Within the limits imposed by these two conditions, the work was designed to answer the following questions:

(i) At which growth stage will glyphosate treatment result in the greatest root kill?

(ii) How effectively is a stem killed when glyphosate is applied to only a small proportion of the foliage?

(iii) How effectively is glyphosate translocated into untreated stems?

(iv) Does the growth stage of an untreated stem affect the amount of glyphosate translocated into it?

(v) How does the position of the treated tissue on a stem affect translocation of the applied glyphosate?

(vi) Is more glyphosate translocated from leaves treated on the upper surface than from leaves treated on the lower surface?

LITERATURE REVIEW

(1) GLYPHOSATE ABSORPTION:

(a) Characteristics:

A herbicide can be absorbed by plants either through the roots or the foliage. However, root absorption is unimportant with glyphosate as it is rapidly adsorbed and deactivated by soil particles (Sprankle *et al* 1975a).

Most foliar absorption of glyphosate takes only a few hours. Haderlie (1975) found that soybean (*Glycine max*) leaves absorbed glyphosate mainly within 6 hr of treatment. Of the total glyphosate that had accumulated in soybeans 48 hr after treatment in another experiment, nearly 50% was present after the first 12 hr (Haderlie *et al* 1978). In *Agropyron repens*, Sprankle *et al* (1975b) showed that glyphosate absorption occurred most rapidly during the first 4 hr after treatment, but continued for 48 hr. At 4, 8, 24 and 48 hr after application, the plants had absorbed 34, 40, 45 and 53% of the applied glyphosate respectively. Absorption of glyphosate in barley has been shown to continue for up to 24 hr, though no further absorption occurred after this time (O'Donovan and O'Sullivan 1982).

C. arvense appears to absorb glyphosate at similar rates. Gottrup *et al* (1976) compared the absorption of glyphosate by *C. arvense* and *Euphorbia esula*. The two species had absorbed similar quantities of glyphosate after 1 week, but whereas *E. esula* absorbed 82% of the final amount 12 hr after application, *C. arvense* absorbed only 47% in the first 12 hr. However, in a second experiment, both species absorbed in the first 12 hr about 33% of the quantity found in them after 1 week. In another experiment with *C. arvense*, Verity (1981) found that almost all glyphosate absorption had occurred within 24 hr of application.

Measurements of the proportion of glyphosate absorbed after application to foliage show great variation. With *C. arvense*, absorption varied from 19% to 89% for Verity (1981), and from 27% to 85% for Gottrup *et al* (1976). Absorption of glyphosate in other species has varied from 10% to 70% in *Cynodon dactylon* (Jordan 1977), 32% to 58% in *Echinochloa crus-galli* (Ahmadi *et al* 1980), and from 23% to 74% in soybeans (McWhorter *et al* 1980). Haderlie *et al* (1978) measured only 7%

glyphosate absorption by soybean.

(b) Factors Affecting Absorption:

Some of the factors known to influence glyphosate absorption are as follows:

(i) Relative humidity and rainfall:

Greater glyphosate absorption occurs when relative humidity is high. Gottrup et al (1976) found C. arvense plants kept under high humidity conditions had absorbed 82% of the applied glyphosate after one week while plants under low humidity conditions absorbed only 27% over the same period. Likewise, Euphorbia esula absorbed 89% of the glyphosate under high humidity and 27% under low humidity in the same experiment.

In a similar trial with Cynodon dactylon, Jordan (1977) obtained 60% absorption of glyphosate at 100% RH (relative humidity) after 48 hr, and only 9% absorption at 40% RH. McWhorter et al (1980) found Sorghum halepense absorbed more glyphosate at 100% RH than at 40% RH. Wills (1978) measured 35% absorption of glyphosate by cotton (Gossypium hirsutum) at 100% RH and only 8% at 40% RH.

High humidity increases foliar absorption of most herbicides, and possible reasons for this include a reduction in drying rate of spray droplets, thus extending the time for absorption; increased stomatal opening, thereby enhancing penetration via this route; and an influence on the degree of leaf cuticle hydration, which in turn influences permeability (Hull 1970).

Glyphosate is highly soluble in water (13,000 ppm at 25 C) (Matthews 1975) so that rainfall during the first few hours after application can result in reduced herbicidal effects due to the glyphosate being washed off the plant (Spurrier 1973). Baird et al (1972) stated that there should be no rainfall for at least 8 hr after glyphosate application to Agropyron repens if reductions in the level of control are to be avoided.

(ii) Water stress:

Water stress reduces glyphosate absorption. Ahmadi et al (1980) found that Echinochloa crus-galli absorbed only 18% of applied glyphosate at 10% soil moisture level, whereas at 40% moisture, absorption was 62%.

Field capacity was at 30% moisture. With Sorghum halepense, an average glyphosate absorption of 55% was obtained at a soil moisture level of 20% (field capacity), compared to 39% at 12% moisture (near wilting point) (McWhorter et al 1980). In the same experiment, soybean plants absorbed 17% of the glyphosate at field capacity and 14% at 12% moisture. Lauridson et al (1980) found glyphosate absorption by C. arvense decreased with increasing moisture stress from -4.3 to -20.1 bars.

Whereas the experiments mentioned so far involved water stress being applied for only a few days before and after glyphosate application, Rashed-Mohassel (1982) applied glyphosate to 100 day-old Convulvulus arvensis plants which were kept at high (field capacity), medium (1/2 field capacity), and low (1/3 field capacity) soil moisture for 35 days before treatment. Low soil moisture caused an increase in cuticle development and leaf thickness, more compact mesophyll cells and increased epicuticular wax deposition. Slightly more (3-9%) glyphosate was absorbed in plants under no stress than in plants under medium or low moisture conditions, and Rashed-Mohassel considered that absorption was not affected enough by moisture conditions to be a major factor in reduced control of this weed by glyphosate applied under conditions of water stress.

Van Overbeek (1956) stated that swelling of polar cutin with an ample water supply would enhance the cuticle's permeability, particularly to water-soluble compounds. However, Hull (1970) reported that, although a favourable water balance is considered important for optimum translocation, many workers have disputed van Overbeek's view that water stress reduces foliar absorption. The situation is unclear.

(iii) Temperature:

Foliar absorption of glyphosate generally increases with temperature, but this relationship is slight in some species and even reversed in others. Lund-Hoie (1979) found that absorption of glyphosate by the brush species Betula verrucosa at 70% RH 1 week after application was 7, 15 and 60% at 12, 18 and 24 C respectively. Temperature levels for the week prior to application also influenced absorption.

Jordan (1977) did not consider temperature to be as important as humidity in its effect on glyphosate toxicity in Cynodon dactylon. He found that at 40% RH, this species absorbed 9% of the applied glyphosate at 22 C and 15% at 32 C; at 100% RH, there was 60% absorption at 22 C and 71% at 32 C.

At 100% RH, an increase in temperature from 22 to 32 C resulted in an increase in glyphosate absorption by cotton plants from 23 to 28% without surfactant and from 36 to 43% with surfactant (Wills 1978). The same experiment conducted at 40% RH did not result in a significant increase in absorption.

McWhorter et al (1980) showed absorption of glyphosate by Sorghum halepense to nearly double as the air temperature at which treated plants were maintained increased from 24 to 35 C. In contrast, they showed absorption to be lower at 35 C than at 24 C for soybean.

Sargent (1965) considers temperature can influence foliar absorption in many ways as it affects both metabolic and non-metabolic absorption mechanisms.

(iv) Light:

Hull (1970) stated that evidence for the effects of light on foliar absorption is conflicting. He blames this confusion on the interaction of light with temperature, humidity, photodecomposition, stomatal closure, and photosynthesis. However, Whitwell et al (1980) found excised Cynodon dactylon leaf tips and stem sections absorbed more glyphosate in the light than in the dark.

(v) Age and position of treated tissue:

Some evidence suggests glyphosate is more easily absorbed by younger plant tissue. Verity (1981) found C. arvense plants at the vegetative stage of growth absorbed about 62% of the glyphosate applied to their leaves, whereas those at the post-flowering stage absorbed an average of 35%. She suggested a lack of trichomes at the older growth stage may have caused the reduction in absorption. Trichomes are thought to aid penetration of herbicides due to having thinner walls and less cuticularization near their bases (Hull 1970). However, large variations existed in Verity's results, possibly because of fluctuations in relative humidity (humidity was not recorded) or because the leaf

surface was broken by the tip of a micropipette during application to simulate damage by a spiny wick.

Pulver and Romero (1976) considered penetration of Cyperus rotundus leaf cuticles by glyphosate, applied at 3 kg/ha, took twice as long in mature plants as in young plants.

Absorption of glyphosate by Echinochloa crus-galli decreased from 58% to 47% as plant height increased from 5 to 15 cm (Ahmadi et al 1980), another indication of reduced absorption by older tissue. Coupland et al (1978) reported that the performance of glyphosate in another grass species, Agropyron repens, was increased when the herbicide was applied towards the leaf or plant base, with treatment of the youngest, fully expanded leaf giving the best performance. They believe that variations in the amount of epicuticular wax between different areas on the leaf could be an important factor determining performance.

Greater tissue activity may also explain increased absorption by younger tissue. Lund-Hoie (1976) found uptake of glyphosate by 4-year-old Norway spruce (Picea abies) plants was four to five times greater when shoots were actively growing than when there was no shoot elongation.

However, other workers have found older tissue absorbs glyphosate best. McWhorter et al (1980) found that absorption in soybeans was greater when the herbicide was applied to mature rather than immature leaves and stems. For the unifoliolate leaf, the first, second and third trifoliolate leaves, and the apical bud, 63, 53, 31, 22 and 11% absorption was measured respectively. Absorption by the lower stem (between the unifoliolate and first trifoliolate leaves) was 50%, while the upper stem (between the second and third trifoliolate leaves) absorbed 29% of the applied glyphosate, ie similar absorption rates to leaves in these areas.

Wills (1978) found stems of cotton plants absorbed more glyphosate than leaves, and that younger tissue absorbed less than older tissue. Apical leaves absorbed 17% of the applied glyphosate compared to 41% by basal leaves. Upper stems showed 70% absorption and lower stems 86%. So although McWhorter et al and Wills obtained contrasting results concerning the relative abilities of stem and leaf tissue to absorb glyphosate, they both measured greater absorption by more mature tissue.

Hull (1970) claims that absorption of most organic and inorganic solutes is generally greater in relatively young leaves. One exception to this he quoted was work done by Kamimura and Goodman (1964). They found that the amino acid leucine was absorbed more readily by older apple (Malus spp) leaves, and suggested that discontinuities and cracks in the cuticle of the older leaves may have been partially the reason for this phenomenon. This is a possible explanation for the findings of McWhorter et al and Wills quoted above.

In experiments with C. arvense, Lish and Messersmith (1979) found glyphosate entered the plant more readily when applied to an upper rather than a lower leaf surface. Likewise, King and Radosevich (1978) found slightly more glyphosate penetrated the upper leaf surface of the woody species Lithocarpus densiflorus than the lower leaf surface. However, it is generally accepted that greater penetration of pesticides and other substances occurs through the lower leaf surface, and the thinner cuticle, greater number of stomata, different structure of epicuticular wax and increased absorptive area due to corrugation of the lower leaf surface are all possible explanations for this increased absorption rate (Hull 1970).

(vi) Species and varietal differences:

Genetic differences can also influence glyphosate absorption by plants. In comparisons of grass species with herbaceous dicotyledons, 73% absorption was recorded by Devine (1981) in Agropyron repens compared with 63% in C. arvense, while McWhorter et al (1980) showed that Sorghum halepense absorbs significantly more glyphosate than soybeans. Investigations with herbaceous dicotyledons have shown differences in absorption to be responsible for the greater susceptibility of Asclepias syriaca compared with Apocynum cannabinum (Wyrill and Burnside 1976), but the susceptible species C. arvense absorbs similar amounts of glyphosate to the tolerant Euphorbia esula (Gottrup 1976). Differences in uptake have also been measured in two brush species, with Fraxinus excelsior absorbing over three times as much glyphosate as Betula verrucosa. Differing absorption rates do not explain susceptibility differences in this example either, however, as F. excelsior is the more tolerant species (Lund-Hoie 1979).

Absorption can also be influenced by genetic differences within a species. McWhorter et al (1980) investigated glyphosate activity in six soybean cultivars, and found that absorption of the herbicides varied from 23 to 74%.

Hodgson (1973) found that the amount of lipid present on leaves of C. arvense varied depending on the ecotype, and he also found a high correlation between ecotypes with large lipid deposits and ecotypes resistant to 2,4-D. Thus differential absorption may be one reason for the variability in susceptibility of C. arvense to glyphosate shown by Saidak and Marriage (1976).

(vii) Adjuvants:

Absorption of glyphosate by C. arvense can be increased by surfactants (Gottrup et al 1976), and similar increases have been noted in Agropyron repens (Sprankle et al 1975b; Erickson 1981), Asclepias syriaca and Apocynum cannabinum (Wyrill and Burnside 1977), cotton (Wills 1978), and soybeans (McWhorter et al 1980). Surfactants with increased ethoxylation and a high hydrophile-lipophile balance are generally the most effective at improving glyphosate absorption (Wyrill and Burnside 1977).

Additions of ammonium sulphate can cause large increases in the phytotoxicity of glyphosate to Agropyron repens, and increased glyphosate uptake induced by the ammonium sulphate is thought to be responsible for this phenomenon (Turner and Loader 1980).

(viii) Leaf surface features:

The nature of a leaf surface can influence its ability to retain applied herbicide long enough for absorption to occur. Gunther and Wortmann (1966) demonstrated that herbicide droplets adhere with much more tenacity to rough-surfaced leaves than smooth, waxy-surfaced cuticles. Likewise, the type and density of trichomes on a leaf surface can affect the retention and absorption of herbicide (Challen 1962).

Glyphosate is susceptible to adsorption by clay colloids (Sprankle et al 1975a) and so Monsanto (1982) have recommended that it should not be applied to plants covered in dust as it could be deactivated before absorption can occur.

Verity (1981) noted that C. arvense leaf surfaces which came into contact with a ropewick applicator suffered considerable mechanical damage, and so considers other factors influencing glyphosate absorption to be of less importance when this method of application is used. Presumably, the damage she observed was inflicted by thistle spines lodged in the wicks, and so damage could only be expected when the wick has been used on prickly plants. Broken stems resulting from passage of the boom itself could affect translocation, but only absorption is being considered in this section.

(c) Absorption Mechanism:

A comprehensive review of foliar absorption mechanisms and of the structural components of leaves through which absorption occurs has been given by Franke (1967). Herbicide molecules penetrating into a leaf must pass in turn through an outer layer of nonpolar, lipophilic waxes; a cuticle composed of cutin, pectins, cellulose and waxes; the epidermal cell wall consisting mainly of cellulose; and finally the semi-permeable plasmalemma lining the epidermal cell. The mechanism of penetration through the cuticle and cell wall for organic and inorganic ions is thought to be a physical process of diffusion. Once this has occurred, it appears these molecules are then adsorbed to the surface of the plasma membrane, after which they are taken up into the cytoplasm of the epidermal cells in a process requiring metabolically derived energy. Understanding of the absorption processes, especially that involving the plasmalemma, is far from complete.

A number of workers have investigated the foliar absorption of glyphosate, a relatively small, hydrophilic, anionic molecule, and their findings in some cases have tended to conflict with the classical view of foliar absorption.

Fernandez (1979) studied the absorption of glyphosate using narrow sections (300 um) of tobacco (Nicotiana tabacum) leaves to allow all intact cells to participate in the absorption process and circumvent the necessity for glyphosate to penetrate cuticular layers prior to cellular absorption. He found that absorption was not inhibited by compounds of similar structure (glyphosine and glycine), was independent of either an energy supply or of temperature, and was proportional to the external concentration of the herbicide. He concluded that glyphosate entered the leaf cells passively by diffusion.

In direct contrast, Leonard and Shaner (1979) showed that glyphosate uptake by tobacco cell protoplasts was energy-dependent, because transport could be inhibited by metabolic inhibitors such as 2,4-dinitrophenol and oligomycin. They concluded that glyphosate was readily transported across plant cell membranes and, as its uptake characteristics were similar to those of leucine, thought the amino acid transport system might be involved.

However, Richard and Slife (1979) consider that cellular absorption represents the major barrier to foliar absorption of glyphosate by Apocynum cannabinum because they showed that the pattern of absorption in isolated cells was similar to the pattern in detached leaves. Their experiments also showed glyphosate to have entirely different uptake characteristics to those of leucine.

Wyrill and Burnside (1976) found that Asclepias syriaca absorbed more glyphosate, and so was more susceptible to this herbicide, than Apocynum cannabinum. They attributed this to A. syriaca having less epicuticular wax, thinner cuticle, a lower contact angle with the herbicide spray, and more stomata and trichomes on the upper leaf surface. However, Wyrill (1976) showed that diffusion of glyphosate through isolated cuticles of A. cannabinum and A. syriaca was unaffected by surfactants. As Wyrill and Burnside (1977) found that surfactants did increase the overall absorption into the leaves, they concluded that the surfactants were affecting the permeability of the plasmalemma, backing up their reasoning with the findings of Sutton and Foy (1971) that surfactants can affect membrane permeability.

Yet Erickson (1981) did find surfactants to cause an increase in diffusion across isolated cuticles of Agropyron repens. She also found that penetration of glyphosate through the cuticle increased in a linear fashion with increased concentration, confirming classical views of passive diffusion being the main process involved in cuticular penetration.

The evidence noted earlier that high humidity increases glyphosate absorption could be an indication of the importance of the cuticle to penetration into leaves, as humidity has been linked with cuticle permeability by some workers (Hull 1970).

King and Radosevich (1978) examined the penetration of glyphosate (10 uM) into leaf discs of Lithocarpus densiflorus, and found that penetration was correlated with certain surface characteristics including cuticle thickness, stomatal density and pubescence.

(2) TRANSLOCATION OF ASSIMILATES:

A number of herbicides such as MCPA, 2,4-D, amitrole, dalapon, barban and maleic hydrazide are transported around the plant in the phloem (Sagar et al 1977). As these herbicides follow the same pattern of movement as assimilates, a study of assimilate translocation can lead to a better understanding of herbicide movement.

(a) Direction of Movement:

Movement of materials in the phloem is often explained by the source-sink concept. This has been defined by Canny (1975):

"The places of manufacture of new organic substance, or the places where it has been stored and is being remobilized, are called the sources: mature leaves, cotyledons or endosperms of germinating seeds, storage tissues of stem, leaf or root when they are sprouting. The places of disposal of the body substance for the formation of new organs or the laying down of reserves, are called sinks: meristems, very young leaves, cotyledons or endosperms of seeds being formed, storage tissues of stem, leaf or root when they are accumulating. The plant functions throughout its life by transferring material from sources to sinks by translocation."

In a study of phloem transport in beans, Biddulph and Cory (1965), using 14-C-carbon dioxide-feeding and fluorescence techniques, have shown that leaves nearest the root transport metabolites primarily to the root. Leaves nearest the top of the plant transport to the stem apex, while leaves in an intermediate position translocate metabolites in both directions.

Sagar et al (1977) have outlined the implications of this concept for phloem-mobile herbicides. Herbicides applied to very young leaves will remain in the leaves as they are not exporting sugars. Herbicides applied to young leaves which have begun exporting sugars will probably

be translocated to the stem apex. The leaves most likely to transport the herbicide down into the roots, often the desired target of the herbicide, are the leaves at the basal part of the stem, and these are the leaves least likely to receive spray. These comments are particularly relevant to herbicides applied by the ropewick applicator.

Devlin (1975) states that several studies of translocation patterns show that materials moving in the phloem ducts generally move in a linear fashion. That is, sugars moving out of a leaf into the main translocation stream will move both up and down the stem in line with the supplying leaf. Very little tangential movement takes place. This was shown by Joy (1964) in a study with sugar beet. When 14-C-carbon dioxide was fed to a leaf, labelled metabolites were found only in leaves directly above or in the root directly below the supplying leaf.

Radial transfer from the phloem to the xylem tissues has been observed in a wide variety of plants (Devlin 1975). In fact, loss of labelled metabolites from the phloem to the xylem through radial transport has been shown in the bean plant to reach values of 49% for metabolites from younger leaves, though values of only 4% were obtained for metabolites from older leaves (Biddulph and Cory 1965). Because of their position as continuous connections between the phloem and the xylem, vascular rays are thought to facilitate radial movement (Devlin 1975).

(b) Sinks in Cirsium arvense:

As was noted by Vanden Born (1980) the transport system in perennial weeds is much more complicated than in annuals, especially with respect to the relationship between growth stage of the plant and translocation to underground roots or rhizomes. In an annual the major translocation sink for assimilates is the shoot tip, whereas perennials have additional sinks in creeping roots or rhizomes, particularly during growth stages when these structures are extending rapidly or when they are giving rise to secondary shoots.

Much of the work on assimilate flow in C. arvense has involved measuring the levels of carbohydrate and nitrogen root reserves of field-grown plants throughout the year. Welton et al (1929), Arny (1932), Bakker (1960), Hodgson (1968), Muller and Ozer (1968), and Otzen and Koridon (1970) have all conducted such studies, mainly to find when root reserves are at their lowest, a stage at which maximum

susceptibility to cultural control measures might be expected.

All of these workers found root reserves to drop sharply during spring while the roots provide a source of carbohydrate and nitrogen for the newly developing stems. The earlier studies suggested that upward translocation stopped, and the minimum level of reserves occurred, once the stems had completed most of their vertical vegetative growth and were entering their reproductive phase of development. Minimum levels have been calculated to occur at the end of rapid vegetative development (Welton et al 1929), at the commencement of flowering (Arny 1932), in early summer (Bakker 1960), and at the early bud stage (Hodgson 1968).

However, Muller and Ozer (1968) calculated this low point to occur at a stem height of 10 cm in plants that reached a final height of 120 cm. They claimed that assimilates were no longer being sent upward during vertical shoot growth but rather were being translocated back down to the roots to replenish the depleted reserves. They backed up this statement by showing MCPA to be translocated to the roots more effectively in stems 20 cm tall than in stems of 70 cm (pre-flowering) or 120 cm (full maturity). Otzen and Koridon (1970) found minimum root reserves to occur 31-49 days before the onset of flowering, the exact time depending on the weather. This estimate agrees more with Muller and Ozers' work than with the earlier reports.

That root reserves are replenished during the later stages of the growing season is agreed upon by all workers. Roles are reversed during this time so that the roots are now the sink for assimilates and the stems the source. This build-up of material is generally thought to continue to the end of the season in late summer or early autumn, though Muller and Ozer found storage declined considerably in their trials shortly after the commencement of flowering. In addition, Muller (1969) found that the major portion of MCPA applied to C. arvense at the flowering or fruiting stage was translocated towards the shoot tip, not the roots.

Sagar and Rawson (1964) stated that, although cultural control methods may be more successful if performed when root reserves are at their lowest, successful control using phloem-mobile herbicides should in theory be achieved at the post-flowering growth stage when maximum translocation of the herbicide into the root system could be expected.

They claimed that C. arvense roots survive no longer than 1-2 years so that destruction of newly formed roots by well-timed herbicide application should enable rapid control of this weed to be achieved. However, they did not conduct field trials to test this theory.

Verity (1981) applied labelled carbon dioxide to the third fully expanded mature leaf from the apex of C. arvense plants approximately 20 cm tall (final stem height was 100 cm) with between 6 and 13 fully expanded mature leaves. Similar quantities of labelled assimilates were subsequently detected in the apical leaves and the roots. She conducted a similar experiment with plants at their full height and with their "oldest flower buds well past full colour". A mature leaf half-way along the main stem was treated in these plants. Approximately four times more label was sent down the stem to the roots and secondary stems than up toward the apex. The label sent upward was found mostly in the stem rather than the leaves, and none was found in the flowers.

Comparisons between Verity's findings and those of other workers should be made with caution as Verity was following movement from particular leaves whereas workers using root reserves were measuring overall assimilate export to the roots. As already mentioned, direction of assimilate export from a leaf depends on how close the leaf is to particular sinks (Biddulph and Cory 1965) so, although one leaf might send most of its assimilates to the roots, leaves higher up the stem could be sending a greater proportion to the apex. Despite this, Verity's results suggest plants were no longer dependent on root reserves once they were 20 cm tall, in agreement with Muller and Ozer (1968). Perhaps Verity's plants, which were grown from 6 cm root segments, had exhausted their root reserves by this growth stage while plants at similar growth stages in other experiments, most of which developed in the field from undisturbed root systems, had not. In contrast, assimilate movement in the post-flowering plants of Verity's experiment followed the pattern postulated by most workers other than Muller and Ozer. Unfortunately Verity did not differentiate between glyphosate sent to roots and to the secondary stems because if most was sent to secondary stems, good control of the roots by herbicides applied at the post-flowering growth stage as predicted by Sagar and Rawson could not be expected.

According to Vanden Born (1980), very little is known about the distribution patterns of assimilates in C. arvense plants with secondary shoots. He mentions reports of assimilates being sent from the parent shoot to some secondary shoots while other secondary shoots connected to the same rhizome were bypassed. No adequate explanation is available for this finding and several attempts to reproduce the results have been unsuccessful.

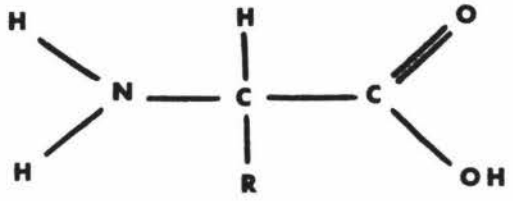
The complexity of assimilate translocation in C. arvense is also indicated by results obtained by Fykse (1977). He found that H-3-labelled saccharose, injected into the mother rhizome/root, was translocated acropetally to the rosette, while 14-C-labelled saccharose injected into the largest rosette leaf of the same plants was simultaneously translocated into both mother and daughter roots/rhizomes. Movement of assimilates, formed by photosynthesis in a 14-C-carbon dioxide atmosphere, into the roots took place in increasing amounts with increasing size of the plants. Only very small quantities of assimilates were stored in the roots. The use of the term "rosette" in the abstract of these experiments suggests the plants used were at an early vegetative stage of growth.

(c) Amino Acid Translocation:

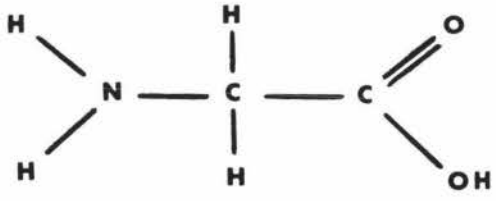
Whereas translocation of hormone type herbicides such as 2,4-D, MCPA, dicamba and picloram is very similar to that of assimilates in C. arvense and most other plants, the pattern of glyphosate translocation has been shown to differ from this pattern in some studies (Vanden Born 1980). Glyphosate is also very different chemically. Whereas the hormone type herbicides are all aromatic compounds, glyphosate is an aliphatic substituted glycine. Figure 1 shows the general structure of an amino acid, and also the structures of glycine and glyphosate. Although not an amino acid, the structure of glyphosate is closer to that of an amino acid than to photosynthetic assimilates, so that it may be of value to consider the transport of amino acids briefly.

The concentration of nitrogenous compounds in the phloem is affected by the different developmental stages of the plant. For example, in the willow Salix viminalis, these compounds are present in highest concentration and variety during rapid leaf growth and at the end of the growing season during leaf senescence (Swanson 1959). Amino acids and amides are translocated out of senescent leaves and flowers and

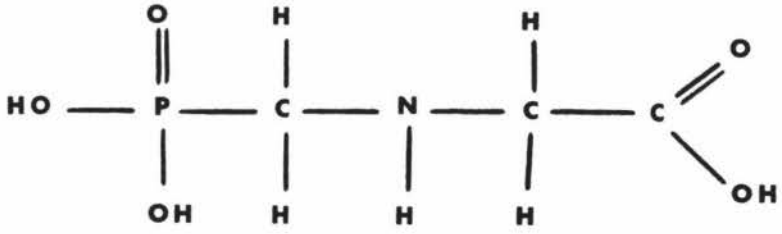
FIGURE 1: Structures of amino acid, glycine and glyphosate.



amino acid



glycine



glyphosate
(N-(phosphonomethyl)glycine)

relocated in other areas of the plant. For most of the season, however, nitrogenous compounds are only present in the phloem in very low concentrations (Devlin 1975).

Welton et al (1929), Arny (1932), and Otzen and Koridon (1970) have all recorded the fluctuations in nitrogenous root reserves of C. arvense. The concentrations never reached more than 3% of the total root dry weight, but were considered important for the production of new stems in spring. These workers all found that root nitrogen levels fell during the phase of rapid stem growth and rose again later in the season, fluctuating in the same manner and at approximately the same times as the carbohydrate levels.

Crafts and Yamaguchi (1964) showed that amino acids can move in both the phloem and the xylem. Some (e.g. DL-valine and tryptophan) travelled only in the phloem, while others (e.g. L-valine) seemed to move as freely in the transpiration stream as they did in the assimilate stream. Yamaguchi and Islam (1967) found glycine to move equally well in the phloem and xylem of Hordeum vulgare var Atlas, while it moved more strongly in the phloem than in the xylem of H. vulgare var Atsel. Amino acids have been shown by a number of workers to be capable of moving between phloem and xylem. For example, Gardner and Peel (1971) found that labelled amino acids fed to the xylem of Salix spp were subsequently recovered in the stylet exudate of aphids feeding on nearby phloem. Although carbohydrate is usually recorded as being absent or present in only trace amounts in the xylem sap of herbaceous species, amino acids and amides are commonly found in this sap (Pate 1975). In plants which manufacture organic nitrogen compounds in their roots from inorganic nitrogen absorbed from the soil, the bulk of this nitrogen is transported to the above-ground parts of the plant as amino acids, amides or ureides, and this occurs predominantly, if not exclusively, in the xylem (Pate 1973).

(3) GLYPHOSATE TRANSLOCATION:

(a) Characteristics:

The majority of workers studying the translocation of glyphosate claim that it moves in the phloem from source to sink in the same manner as assimilates. This has been observed in Cirsium arvense, Convulvulus

arvensis, Amaranthus retroflexus, soybean, maize, Agropyron repens, Cyperus esculentus (Sprankle et al 1975b); Cynodon dactylon (Fernandez and Bayer 1977); cotton (Wills 1978); Ipomoea purpurea, Convulvulus sepium, Polygonum convulvulus (Sandberg et al 1980); Apocynum cannabinum (Schultz and Burnside 1980); and Oxalis pes-caprae (Campbell et al 1981b). Glyphosate was translocated to areas of highest metabolic activity in these species, usually shoot tips and new roots. Sandberg et al (1980) found glyphosate was localized in the phloem of stems and roots of several species. Martin and Edglington (1981) compared the movement of sucrose and glyphosate in soybean and barley and found they were translocated in a similar pattern.

However, a few workers consider that glyphosate also travels in the apoplast. Gottrup et al (1976) found that, although glyphosate moved via the symplast to the roots and young growing leaves of C. arvense and Euphorbia esula, there was also movement via the apoplast to the margins of the treated leaf. Verity (1981) confirmed this apoplastic movement in C. arvense by finding labelled glyphosate in the spines and margins both of treated and nearby untreated leaves. She commented that the spines appeared to be acting as guttation ducts with tiny droplets developing at the tips.

Dewey (1981) compared the translocation patterns of leaf and stem applications of 14-C-glyphosate and 14-C-carbon dioxide (as assimilate) in Ipomoea purpurea. The results suggested that glyphosate moved readily via the symplast from assimilate source to sink. However, a substantial portion of the applied herbicide also appeared to be transported via the transpiration stream to all transpiring tissues above the site of application. Glyphosate could transfer from the apoplast to the phloem with relative ease, while the herbicide had a tendency for limited leakage from the phloem back to the apoplast. In a study of glyphosate translocation in 4-year-old Norway spruce (Picea abies) plants, Lund-Hoie (1976) found translocation took place mainly in the phloem, but there was some lateral migration to the xylem and accumulation in transpiring tissue. Glyphosate was also found to move into the xylem of the brush species Fraxinus excelsior, yet under the same conditions it remained mainly in the symplast of Betula verrucosa, also a brush species (Lund-Hoie 1979).

Eliasson (1965) obtained evidence that 2,4-D also travels in both the xylem and the phloem. He stated that, although the extent to which 2,4-D is transferred from phloem to xylem may vary from one species to another, the reason why most workers to that date had not observed apoplastic movement of 2,4-D was probably because the concentrations of labelled herbicide they used were far too low. He considered it probable that 2,4-D in the low concentrations resulting in the tissues from such applications would probably be retained in living cells to a greater extent than the concentrations used in herbicidal applications. In most of the glyphosate studies cited above very low doses of herbicide were used, except in that by Verity who used a moderately high dose. Unfortunately the dosage used by Dewey is not cited in the abstract of his work, but Lund-Hoie (1979) used only low doses.

The velocity of glyphosate translocation does not appear to have been measured, but relatively rapid translocation rates varying from 40 to 290 cm/hr have been recorded for assimilates in the phloem of several species (Devlin 1975). It is difficult to separate the time for absorption from the speed of movement in most glyphosate translocation studies. Ghanuni (1981) reported that glyphosate was translocated throughout Convulvulus arvensis plants within 2.5 hr of application. Gottrup et al (1976) detected glyphosate in the roots of C. arvense within 1 hr of application. Sprankle et al (1975b) measured glyphosate levels of 9, 26, 49 and 67% of the amount applied in untreated rhizomes and shoots of Agropyron repens 4, 8, 24 and 48 hr after application respectively. Of the glyphosate that had been absorbed by barley 12 hr after application, 54% of it had translocated out of the treated leaf (O'Donovan and O'Sullivan 1982). So it seems that glyphosate can move rapidly since it is found throughout plants soon after application, but it also appears that absorption and/or translocation from treated tissue continues for some time.

Sandberg et al (1980) found that almost no further translocation of glyphosate out of the treated leaf itself occurred in 14 to 18 cm C. arvense plants after 3 days. However, there was significant basipetal translocation of the herbicide between 3 and 14 days after treatment, apparently due to redistribution of the glyphosate initially translocated acropetally. At 3 days, 48% of the absorbed glyphosate was in the region above and 14% below the treated leaf, while the roots contained 22% and daughter shoots 17%. However, at 14 days after

application, only 25% remained above the treated leaf and 4% below it, while there was 33% in the roots and 38% in the daughter shoots. Further translocation of glyphosate after 3 days was also detected in Polygonum convulvulus, but not in Convulvulus arvensis, Convulvulus sepium or Ipomoea purpurea.

Not all of the absorbed glyphosate is translocated out of a treated leaf, and the proportion that is translocated out varies considerably. Of the glyphosate absorbed by a treated leaf, 92% moved out of the leaf with Cynodon dactylon (Jordan 1977), 75% and 61% moved out in Euphorbia esula and Cirsium arvense respectively (Gottrup et al 1976), 58% and 44% in soybean and Sorghum halepense repectively (McWhorter et al 1980), and 21% in Echinochloa crus-galli (Ahmadi et al 1980). Verity (1981) found only 8% of the absorbed glyphosate moved out of treated C. arvense leaves at the vegetative growth stage, compared with 41% at the post-flowering stage. For both growth stages, 27% of labelled assimilates were translocated from the leaf. Note that Jordan, Gottrup et al and McWhorter et al all used very low doses of glyphosate (9-23 ug), Ahmadi et al used a moderate dose (approximately 0.4 mg), and Verity used a high dose (12 mg), suggesting that high concentrations may reduce translocation.

(b) Factors Affecting Glyphosate Translocation:

(i) Temperature:

McWhorter et al (1980) found that progressively less absorbed glyphosate had been translocated out of treated leaves of both soybean and Sorghum halepense after 72 hr as the air temperature was increased from 24 C to 35 C. Erickson (1981) showed that more glyphosate was translocated in Agropyron repens at 21 C than at either 11 or 32 C. Devine (1981) found that glyphosate was translocated at slower rates in both C. arvense and A. repens at 10 C than 21 C, but that there was ultimately no difference in the total amount translocated after a period of 5 days.

Most studies of assimilate translocation have shown that the rate of translocation increases with temperature to a maximum and then decreases due to the detrimental effects of high temperature (Devlin 1975), and the papers cited above suggest such a relationship also exists for glyphosate translocation. In an experiment with sugarcane (Saccharum officinarum), Hartt (1965) showed that an increase in root temperature

over shoot temperature increased downward assimilate translocation, and that upward translocation was increased if shoot temperature was higher than root temperature. Movement of assimilates into and out of the phloem is controlled by metabolic processes, and temperature is thought to influence translocation rates by affecting these processes (Devlin 1975).

(ii) Water stress:

Translocation can also be reduced by water stress. Ahmadi et al (1980) found that glyphosate translocation was greatly reduced in Echinochloa crus-galli at a soil moisture level of 10% (field capacity = 30%). Reductions in glyphosate translocation by Sorghum halepense and soybeans were recorded by McWhorter et al (1980) as the soil moisture level dropped from 20% (field capacity) to 12% (near wilting point). Translocation of glyphosate to the growing point of C. arvense in the laboratory was shown by Lauridson et al (1980) to remain the same with increasing moisture stress from -4.3 to -20.1 bars, whereas translocation to the roots was markedly reduced. They also found that control of this weed in the field by glyphosate at the bud stage was reduced with increasing moisture stress from -7.6 to -16.3 bars.

Crafts and Crisp (1971) have reviewed a large number of experiments which have also shown a decrease in translocation of phloem-mobile pesticides with water stress. They consider the increased viscosity of the assimilate stream under conditions of severe water stress could explain these observations.

(iii) Light:

Light intensity can apparently affect both the rate and direction of glyphosate translocation. Schultz and Burnside (1980) found that twice as much glyphosate moved into the untreated part of an Apocynum cannabinum leaf after 12 days at a light intensity of 75 klux as at 50 klux, whereas more glyphosate moved to the roots and the stem below the treated leaf at the lower light intensity. In contrast, more 2,4-D was found in the untreated part of the leaf at 50 klux and in the roots at 75 klux in the same experiment. Devine (1981) found that glyphosate was translocated more slowly in Agropyron repens at lower than higher irradiance levels, but he considered that this would probably not ultimately affect the amount exported to the rhizomes. Kells and Rieck (1978) reported significantly greater accumulation of glyphosate in the

roots and rhizomes 6 days after application to the leaves when Sorghum halepense plants were exposed to full light than when kept in the dark. They considered this to be the result of an increased rate of photosynthesis and therefore greater photosynthate movement.

As might be expected, assimilate translocation is affected in similar ways. In wheat Nelson (1963) detected an increase in the proportion of assimilates translocated to the roots compared to the shoots as light intensity increased. Nelson and Gorham (1957) obtained evidence that translocation of assimilates to the roots is favoured over translocation to the shoots of soybean in the dark. Butcher (1965) showed assimilate translocation by sugar beet occurs at a slower rate in the dark.

(iv) Age and position of treated tissues:

Translocation of glyphosate from mature basal leaves differs to that from young apical leaves. Although older soybean leaves were found to absorb more 14-C-glyphosate than younger leaves (McWhorter et al 1980), the proportion translocated out of the treated leaves was smaller so that similar total quantities entered the untreated part of the plant. However, in a similar experiment using unlabelled glyphosate, they found that treatments applied to older leaves caused much greater damage than those applied to younger leaves. The explanation suggested was that translocation of unlabelled toxic substances may have been occurring in the first experiment. Note, however, that glyphosate concentrations of 9 ug/plant were used in the labelling experiment, compared with 1000 ug/plant in the second experiment. The higher concentrations in the second experiment may have changed the tranlocation pattern.

In a similar experiment on cotton Wills (1978) also reported greater damage from glyphosate application to older, basal leaves than to younger, apical leaves. Application to the stem caused even more damage, with applications to the lower stem being more effective than upper stem applications. Autoradiograms showed that glyphosate effectiveness was related to its distribution. Applied to the lower stem, glyphosate was found in the roots and throughout the foliage, whereas applied to an apical leaf it remained almost entirely within this leaf. Although translocation from the lower stem was mainly symplastic, resulting in accumulation of herbicide mainly in the apical leaves and roots, trace amounts also moved apoplastically into mature leaves and the cotyledons.

Comparisons of translocation from stem and leaf applications were also made by Dewey (1982) who found glyphosate had a greater tendency to enter the xylem of Ipomoea purpurea when applied to the stem rather than to leaves. Application to the stem resulted in movement to all transpiring tissue above the site of application, though large amounts also moved downwards in the phloem. A small amount of apoplastic movement occurred after application to the leaves.

Greater translocation to underground plant parts from lower leaves has been noted in several species. Schultz and Burnside (1980) found that glyphosate applied to the lower leaves of Apocynum cannabinum was translocated mainly into the roots, although there was some accumulation in newly developing leaves. More was found in the developing leaves when the herbicide was applied to an upper leaf. Consequently when applied to the upper leaves there was less accumulation in the roots than when applied to the lower leaves, though the glyphosate level in the roots continued to rise for 12 days following the apical application whereas translocation to the roots ceased after 12 hr following the basal application. They also found that up to 20% of the applied glyphosate was exuded from the roots into a nutrient solution.

Likewise glyphosate applied to the lowest two leaves on potato stems resulted in greater reductions in the subsequent production of tubers than when applied to the upper leaves (Lutman 1979). However, similar symptoms appeared throughout the treated stem, including death of apical leaves, regardless of position of application.

Assimilate movement, and thus glyphosate translocation, from one shoot of a perennial plant to another can depend on the maturity of the shoots. Rioux et al (1974) demonstrated that, when one of two Agropyron repens shoots of a similar stage of growth growing from the same rhizome was sprayed, growth of the untreated stem was inhibited by glyphosate applied at the two-leaf but not at the four-leaf stage. Similarly, the growth of tillers was inhibited when only the mother shoot was sprayed. However, when only tillers were sprayed, growth of the mother shoot was not affected.

While translocation of glyphosate from tissues of different ages on the same plant can vary, translocation patterns in plants of the same species but at different stages in their life cycle can also differ.

After experiments with Echinochloa crus-galli, Ahmadi et al (1980) concluded that less translocation occurs in older plants. However, the differences were not large. In contrast, Pulver and Romero (1976) claimed that translocation of glyphosate from foliage to tubers in Cyperus rotundus was more rapid in mature plants. After application at 1.5 kg/ha translocation was completed in 5 days in mature plants but took 15 days in young plants. In the same species Zandstra and Nishimoto (1977) showed increased translocation to developing tubers compared with leaves, flowers or roots as the plant got older. Note that E. crus-galli is an annual and C. rotundus a perennial, so translocation patterns in these two species would be expected to differ at maturity.

An ealier section showed how the relationship between translocation of assimilates and growth stage in C. arvense is complex, and Vanden Born (1980) reports that attempts to relate translocation of glyphosate to growth stage in this species have also been mostly unsuccessful. Using an autoradiographic technique Sprankle et al (1975) found greater movement in C. arvense after application to vegetative plants 10 to 15 cm tall than to plants at the bud to flowering stage. Verity (1981), however, found translocation to be poor in 20 cm tall plants and much better at the post-flowering stage. She measured an average accumulation of 3% of the recovered glyphosate in the roots of vegetative plants compared to 25% in the roots and associated daughter stems of the post-flowering plants. Most other glyphosate translocation studies in C. arvense have used only young plants. Young et al (1977) found that 4% of applied glyphosate accumulated in the roots of 10 week old plants at the bud stage. Sandberg et al (1980) measured levels of 3% in the roots of 14 to 18 cm plants, and a further 3% which passed through the roots to daughter stems. Both Young et al and Sandberg et al obtained results similar to Verity, but Gottrup et al (1976) found that 15% of applied glyphosate was translocated to the roots of 6 to 8 week old C. arvense plants, a considerably higher value than recorded by the other workers for young plants though still much lower than measured by Verity in post-flowering plants.

The extent of translocation at different growth stages may also be indicated by the effectiveness of the application. Marriage (1980) reported that, although glyphosate has given good control of C. arvense over a wide range of growth stages, the bud to bloom stage generally

offers the best and most consistent results. Whereas only 50% control has been obtained from glyphosate application at the emergence and rosette stages, 80-90% control of vegetative plants taller than 8-10 cm, and 90-99% control at 15-20 cm, have been recorded. Post full bloom applications have been reported to be more effective than post bud treatment by Carson and Bandeen (1973), although applications at the mature seed stage have been found ineffective (Lee 1973).

(v) Species and varietal differences:

Sprankle et al (1975b) and Sandberg et al (1980) both compared the behaviour of glyphosate in a number of annual and perennial plants, and found translocation in all species to be similar, in that accumulation occurred at active assimilate sinks. However, there were considerable differences in the position and activity of sinks between species.

As mentioned earlier, there is considerable genetic variability in C. arvense, and in other species such variability has been found to influence glyphosate translocation. The proportion of absorbed glyphosate that was translocated out of the treated leaves of six soybean cultivars varied from 39% to 70%, depending on the cultivar (McWhorter et al 1980). Westra (1981) found that Agropyron repens biotypes tolerant of glyphosate accumulate more glyphosate in the internodes and less in the rhizome buds than susceptible biotypes.

(vi) Herbicide rate and concentration:

Marriage (1980) stated that lower rates of glyphosate can give greater percentage translocation into C. arvense roots than higher rates over the same time period, and they suggested that shoot damage may develop too rapidly at higher rates, restricting translocation.

Translocation studies with radiolabelled herbicides generally use much smaller quantities of herbicide per plant than would be applied in the field. Several workers have compared the translocation of 14-C-glyphosate in plants with and without the addition of larger quantities of unlabelled herbicide to see if increased dosage affects the translocation patterns. Zandstra and Nishimoto (1977) found no difference between the distribution of 14-C-glyphosate (11 ug) in Cyperus rotundus plants sprayed with 2 kg/ha unlabelled glyphosate and that in unsprayed plants. However, the former plants were not sprayed until the labelled 14-C-glyphosate had dried, so absorption and possibly

much of the translocation of the labelled material would have occurred before the herbicidal effects of the subsequent application could develop.

Schultz and Burnside (1980) conducted a similar experiment with both 14-C-glyphosate and 14-C-2,4-D on Apocynum cannabinum, but they applied the labelled material immediately after spraying with the respective unlabelled herbicides. They concluded that absorption and translocation of either labelled herbicide was unaffected by the addition of unlabelled material, but they used only sublethal rates (0.04 kg/ha) so again a valid comparison of translocation patterns obtained in typical labelling experiments and in the field situation was not achieved.

In another experiment of this type, Gigax et al (1976) found that uptake and translocation patterns of 14-C-2,4-D were different in Cirsium arvense, Convulvulus arvensis and Euphorbia esula plants sprayed with 1 kg/ha of unlabelled 2,4-D compared with unsprayed plants. Schultz and Burnside (1980) considered the difference between their results and these was related to the species used, but it seems more likely that the differences in rate of application could be responsible.

The experiments summarised above dealt with the effects of different doses (quantity per plant) on translocation. Another factor which could affect translocation is the concentration of glyphosate applied to foliage. Herbicide applied from a ropewick applicator is much more concentrated than that applied in a spray, and it seems possible that highly concentrated chemical could damage plant tissue so quickly that translocation is impeded. This was indicated by Lish and Messersmith (1979) who applied the same quantity of glyphosate to C. arvense leaves over areas of 0.25, 1.00 and 2.25 sq cm, and found that more herbicide was translocated out of the treated leaf as the size of the treated area increased, ie as the concentration (quantity per unit area) decreased.

(vii) Adjuvants:

If a systemic herbicide is used in combination with a herbicide which causes contact injury to foliage, translocation may be inhibited (Ashton and Crafts 1973). Such inhibition has been observed with glyphosate when it was applied to C. arvense which had already been treated with 2.24 kg/ha of bentazon (Sprankle et al 1975b). Likewise, picloram (0.035-0.07 kg/ha) applied to C. arvense with glyphosate (0.42-1.0

kg/ha) resulted in increased foliar damage and decreased root kill, apparently due to glyphosate translocation being inhibited by the picloram (O'Sullivan and Kossatz 1982).

Although the use of surfactant caused increased absorption of glyphosate by soybeans, McWhorter et al (1980) found surfactant also caused less glyphosate to be translocated out of the treated leaf. In contrast, the addition of potassium dihydrogen phosphate did not increase absorption of glyphosate but did increase its translocation.

(4) METABOLISM OF GLYPHOSATE:

Most workers have found little, if any, metabolism of glyphosate in plants. Gottrup et al (1975), for example, found no metabolites of glyphosate in C. arvense or Euphorbia esula one week after treatment. Other species in which no breakdown has been detected include Asclepias syriaca and Apocynum cannabinum (Wyrill and Burnside 1976); Cyperus rotundus (Zandstra and Nishimoto 1977); Phalaris arundinacea and Festuca rubra (Marquis et al 1979); avocado (Persea persea) (Monsanto 1979); and barley (O'Donovan and O'Sullivan 1982).

On the other hand metabolism has been found in a few cases. Lund-Hoie (1976) observed rapid metabolism, with subsequent detoxification, of 14-C-glyphosate in mature plant parts of 4-year-old spruce (Picea abies, a species which is fairly resistant to glyphosate. He also found that 30-40% of 14-C-glyphosate absorbed by Betula verrucosa was lost as 14-C-carbon dioxide during the 2 months following application (Lund-Hoie 1979). In work by Sandberg et al (1980) little, if any, metabolism of 14-C-glyphosate to aminomethylphosphonic acid, glycine or sarcosine was observed in Cirsium arvense, Convulvulus arvensis or Ipomoea purpurea. However, whereas in Convulvulus all the 14-C could be accounted for after 30 days, in Cirsium only 21% could be found in this period and in I. purpurea only 26% after 21 days. Metabolism of the 14-C glyphosate to a volatile 14-C-metabolite (possibly carbon dioxide) was suggested as an explanation for this loss. Note that, although Gottrup et al (1975) detected no metabolism of glyphosate in Cirsium arvense, they used an experimental period of only 7 days compared to the 30 days used by Sandberg et al.

(5) MODE OF ACTION:

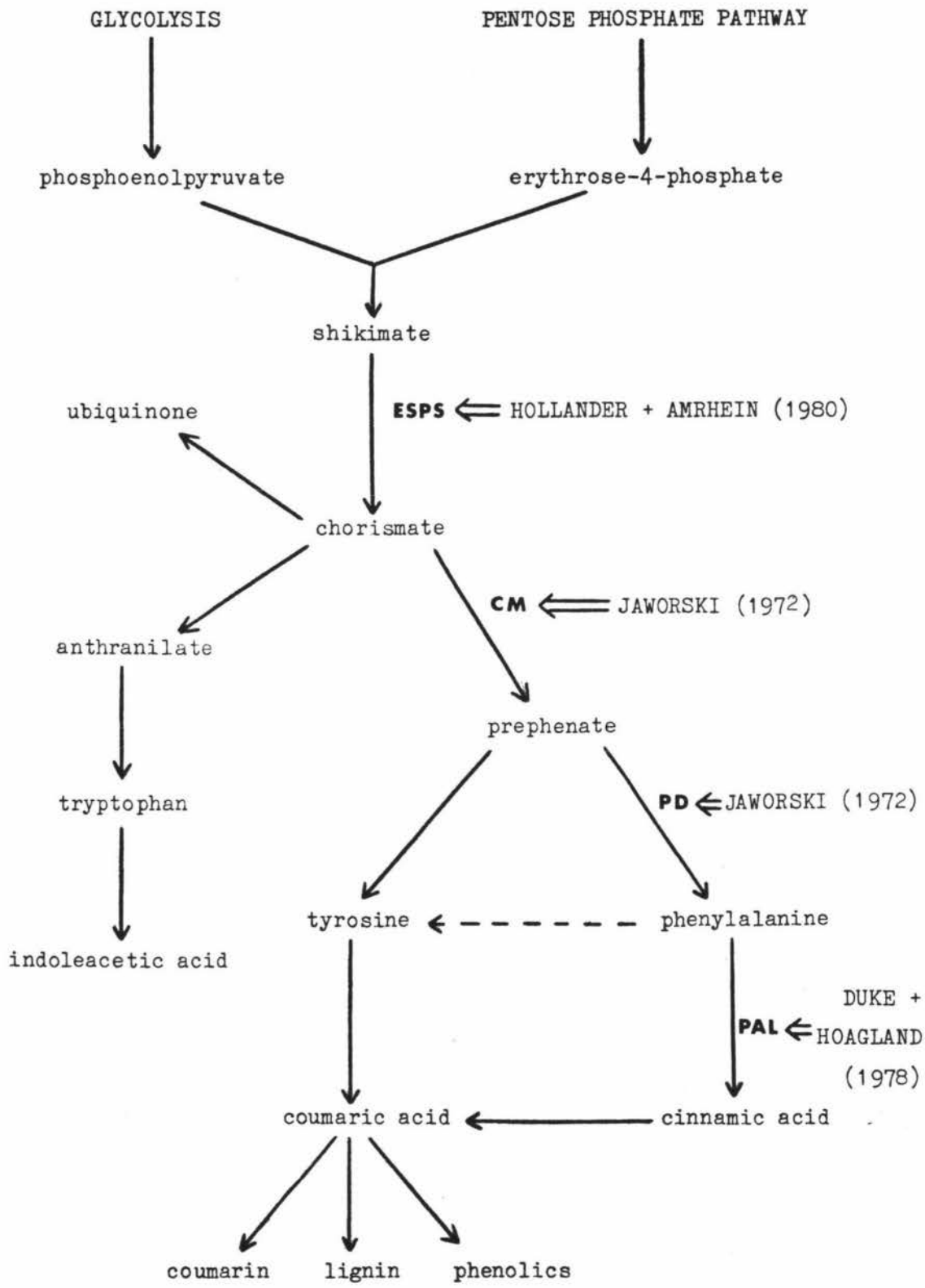
Glyphosate has been observed to disrupt chloroplasts, membranes, and cell walls (Hoagland and Paul 1978); to alter protein and nucleic acid synthesis (Tymonko and Foy 1978); to reduce photosynthesis (Sprankle et al 1975b) and respiration (Tymonko 1979); and to reduce chlorophyll (Kitchen et al 1981), anthocyanin (Hoagland 1980) and hydroxyphenolic (Hoagland et al 1978) accumulation. However, none of these effects are thought to represent the primary mode of action.

Early investigations of the action of glyphosate in plants by Jaworski (1972) indicated that it lowered levels of aromatic amino acids, especially phenylalanine and tyrosine. Aromatic amino acid depletion could cause reduced protein synthesis, cessation of growth, cellular disruption and death. Supplemental aromatic amino acids reversed the growth inhibition, so Jaworski suggested chorismate mutase and/or prephenate dehydratase as sites of repression and/or inhibition (see Figure 2 for diagram of biosynthetic pathways involved).

Some later data supported this theory (Haderlie 1975), but many enzymes of the aromatic biosynthetic pathway were found to be insensitive to glyphosate (Roisch and Lingens 1974). Also, supplemental aromatic amino acids were not antidotal to all systems, especially to intact terrestial plants (Duke and Hoagland 1978). Glyphosate also increases extractable phenylalanine ammonia-lyase activity which could partially explain reduced phenylalanine and tyrosine pools and possibly cause toxicity by increasing ammonia and phenolic acid levels (Duke and Hoagland 1978).

Recently, glyphosate was found to increase shikimate pools by inhibiting the conversion of shikimate into phenylalanine, tyrosine and tryptophan (Hollander and Amrhein 1980). One enzyme involved here, 5-enolpyruvyl-shikimate-3-phosphate synthase, was inhibited by low glyphosate levels and was suggested as a probable site of action by Amrhein et al (1980). Note that inhibition of this enzyme would lead to reductions in levels of indoleacetic acid, an important growth hormone, and ubiquinone, an electron carrier needed for respiration.

FIGURE 2: Outline of aromatic amino acid biosynthesis, including the sites of glyphosate action proposed by various workers. ESPS = 5-enolpyruvyl-shikimate-3-phosphate synthase; CM = chorismate mutase; PD = prephenate dehydratase; PAL = phenylalanine ammonia-lyase. (Adapted from Gresshoff 1979).



(6) GLYPHOSATE SYMPTOMS AND DAMAGE:

(a) Effects:

(i) Pigments:

A common but not invariable symptom of glyphosate action is chlorosis. Fernandez and Bayer (1977) noted this effect in Cynodon dactylon and used the intensity of chlorosis as an indicator of the glyphosate concentration in leaves. Verity (1981) noted chlorosis in the young leaves and regrowth of C. arvense treated at the vegetative stage but not at the post-flowering stage. Saidak and Marriage (1976) also observed little chlorosis in C. arvense treated at the bud stage. In potatoes Lutman and Richardson (1978) found that the young leaves became chlorotic within 3 days of glyphosate treatment, and the symptoms subsequently became more widespread. Yellow veining has been noted as a symptom on the foliage of "Carrizo" citrange (Citrus sinensis x Poncirus trifoliata) seedlings, but not on rough lemon C. jambhiri or sour orange C. aurantium (Tucker 1977). Interveinal chlorosis was described on the lateral shoots of grape vines (Vitis vinifera) developing after glyphosate application (Lee and Cahoon 1981).

In Cyperus rotundus, Abu-Irmaileh (1977) found that treated leaves were a lighter green than untreated 24 hr after spraying with commercial glyphosate, and the leaves turned yellowish and began wilting after 48 hr. The younger leaves were affected more than mature leaves. After treatment in another experiment with a different form of glyphosate (isopropylamine salt), bleached areas developed at the base of the younger leaves (in the region of the intercalary meristems) in 24-28 hr. The veins then became discoloured and eventually looked like white striations. Abu-Irmaileh also noted that chloroplast disruption occurred as the symptoms developed but that darkness decreased or delayed the appearance of the effects. Hoagland and Paul (1978) give an account of the progressive destruction of chloroplasts in treated Cyperus rotundus leaves. They noted visible chlorosis at 48 hr. Campbell et al (1976) described the chloroplast destruction that occurred in glyphosate treated Agropyron repens leaves. Yellowing became evident within 72 hr with rates of 2.2 and 4.5 kg/ha and in 120 hr with 0.6-1.7 kg/ha.

Uotila et al 1980) noted yellowing and chloroplast destruction in Sinapsis alba seedlings. At 5.0 kg/ha, a mild chlorosis was observed 2 days after application, and this intensified after 3-4 days. However, although chlorophyll levels decreased in these plants, treatment with a sub-lethal dose of 0.5 kg/ha increased the chlorophyll level. Abu-Irmaileh and Jordan (1978) measured decreases in chlorophyll levels in treated Cyperus rotundus leaves, while Lee (1981) measured similar decreases in soybean and tobacco. Both thought it possible that glyphosate affected the synthesis of chlorophyll as well as causing its degradation.

Chlorophyll is not the only plant pigment affected by glyphosate. Abu-Irmaileh and Jordan (1978) showed that the level of carotenoids in Cyperus rotundus is also reduced and that it is reduced more rapidly than the chlorophyll level. Anthocyanin levels have been reduced in soybean seedlings (Hoagland 1980) and Fagopyrum esculentum (Amrhein et al 1980), though Uotila et al (1980) reported increases in anthocyanins in the stems of Sinapis alba 12 days after treatment with sub-lethal doses. Red coloration has also been noted in the vestigial leaves and buds of glyphosate-damaged raspberry plants (Clay 1972), and Fernandez and Bayer (1977) observed orange coloration on some parts of treated Cynodon dactylon foliage. These effects may have been caused by red and orange pigments becoming more obvious with chlorophyll removal.

(ii) Necrosis:

Spurrier (1973) states that the chlorosis of foliage affected by glyphosate advances to complete browning and deterioration of plant tissue. Necrosis has been observed to follow chlorosis in Cynodon dactylon (Fernandez and Bayer 1977), potato (Lutman and Richardson 1978) and Sinapis alba seedlings (Uotila et al 1980), though necrosis does not necessarily follow chlorosis in lightly affected tissue (Fernandez and Bayer 1977).

However, Saidak and Marriage (1976) and Young et al (1977) both reported necrosis on leaves and stems of C. arvense several days after glyphosate treatment without preliminary chlorosis. The necrosis became progressively more extensive and severe, and resulted in complete death of the shoots in less than one month with doses above 25 mg ai/plant. Verity (1981) also found necrotic lesions on treated C. arvense leaves 2 days after treatment of plants at the vegetative or post-flowering

stages without preliminary chlorosis, although small brown lesions, coupled with slight bleaching, did occur on young untreated leaves in the vegetative plants. Necrosis without chlorosis appeared to be a contact effect of glyphosate in these trials.

In addition to leaves, glyphosate has been reported to cause necrosis in such tissues as fruit, bark, roots and rhizomes. Tucker (1977) observed that citrus fruit sprayed with glyphosate became "burnt". Rom et al (1974) found necrosis extended from treated apple leaves into nearby branches and trunks. Saidak and Marriage (1976) found necrosis of the roots of C. arvense 2 weeks after glyphosate application to foliage. Rioux et al (1974) noted Agropyron repens rhizomes had become black 4 weeks after foliar treatment. The decay began on buds and continued into the rhizomes.

(iii) Wilting:

Spurrier (1973) considered that gradual wilting and yellowing of a plant were the first symptoms of glyphosate action, and this was observed by Abu-Irmaileh (1977) in Cyperus rotundus. Although Lee and Cahoon (1981) found wilting to be the first symptom on young treated grape leaves, the effect was less apparent on older leaves. Lutman and Richardson (1978) did not observe wilting of treated potato foliage until chlorosis had become extensive and necrosis was developing. On lightly affected potato plants Lutman (1979) did not observe wilting but plants with dead stem apices showed wilted and necrotic older leaves. Verity (1981) noted that the treated leaves of C. arvense appeared to be under severe water stress 2 days after application of glyphosate when necrosis was also appearing. However, Saidak and Marriage (1976) found very little wilting of C. arvense (as well as little chlorosis).

The cause of wilting following glyphosate treatment is poorly understood. Brecke and Duke (1980) found that the guard cells of bean leaves closed within 1 hr of glyphosate application, but although transpiration was reduced, a higher water content resulted in the leaves and so they did not wilt. Crowley and Prendeville (1980) found that glyphosate increased the permeability of leaf cells in bean, but only at high concentrations and not until after wilting had occurred.

(iv) Growth rate:

Glyphosate reduces the growth of a wide range of crops and weeds, as measured by effects on vegetative growth in Cyperus rotundus (Abu-Irmaileh 1977), Cynodon dactylon {Fernandez and Bayer 1977), maize (Hoagland et al 1978), Imperata cylindrica (Moosavi-Nia and Dore 1979), and grape (Gur et al 1979); root growth in grape (Lee and Cahoon 1981); rhizome growth in I. cylindrica (Moosavi-Nia and Dore 1979); and leaf expansion in apple (Curtis 1974), soybean (Baur et al 1977), and bean (Brecke and Duke 1980). Uotila et al (1980) found elongation of Sinapis alba seedlings decreased immediately after being sprayed with 5.0 kg/ha of glyphosate, although 0.1 kg/ha caused an increase in seedling elongation.

(v) Axillary bud development:

Uotila et al are not the only workers to have found an increase in growth caused by low rates of glyphosate. Casely (1972) found that sub-lethal doses of glyphosate applied to Agropyron repens inhibited the growth of existing shoots but caused prolific sprouting from the nodes on aerial shoots so that shoot number and fresh weight were significantly increased compared with controls (Coupland and Casely 1975). Baur et al (1977) also measured greater fresh weight production in sorghum due to stimulation of basal bud development by low glyphosate doses. Similar stimulation of lateral growth was noted in grapevines by Lee and Cahoon (1981) who compared the effect of treating the apical leaves with that of physical removal of the tip. When leaves closer to the roots were treated lateral shoots did not develop though terminal shoot growth was severely reduced. Dormancy breaking and proliferation of axillary buds by low doses of glyphosate have also been noted in potato (Lutman and Richardson 1978), highbush blueberry (Vaccinium corymbosum) (Hodges et al 1979), apple (Clay 1972), and other trees and vines (Lange and Schlesselman 1975).

Lutman (1979) considers that the apical buds of potato are killed after acting as a sink for glyphosate and that the axillary buds are released from apical dominance. He noted death of the stem apex as the commonest symptom of damage in this species. However, Baur et al (1977) found that in sorghum plants with glyphosate-induced proliferating basal buds the apical buds were still active. He suggested that the proliferation might be due to the inhibition of indoleacetic acid biosynthesis resulting from tryptophan deficiencies caused by the treatment.

(vi) Regrowth:

Perennial plants which survive glyphosate treatment often show greatly reduced regrowth capacity in the following season. A significant decrease in the number and weight of regrowth shoots of C. arvense was noted by Saidak and Marriage (1976) and reductions have been reported in the viability of surviving potato tubers (Lutman and Richardson 1978) and Convulvulus arvensis rhizomes (Davison and Bailey 1974).

The regrowth that does occur after glyphosate treatment is often weak and abnormal. Saidak and Marriage (1976) reported that Cirsium arvense regrowth was pale green, had narrow strap-like leaves, and made little growth after emergence. Verity (1981) also described the regrowth of this species as being malformed with thin, strap-like leaves, thick stems, a dull chlorotic colouring and weak growth.

In Agropyron repens an application rate of 0.28 kg/ha significantly reduced rhizome bud survival, while 0.56-1.12 kg/ha gave nearly complete bud kill (Claus and Behrens 1976). In the same species Casely (1972) noted that the new leaves appearing after treatment were diminutive, misshapen and sometimes chlorotic. In environments favouring glyphosate activity (low temperature, high humidity), the shoots made little growth and died, while under glasshouse conditions favouring regrowth, successive leaves were increasingly normal, eventually becoming indistinguishable from those of untreated controls.

In potato the sprouts produced by tubers from treated plants are often deformed, with a cauliflower-like appearance of multiple sprouts and no main axis as described by Lutman and Richardson (1978). Convulvulus arvensis regrowth appears as small dense clumps of miniature leaves the year after treatment (Davison and Bailey 1974).

On other species, the new leaves developing after glyphosate treatment have been described as being strap-shaped, and sometimes cup-shaped, on citrus seedlings (Tucker 1977), severely malformed with interveinal chlorosis and necrosis on grape vines (Lee and Cahoon 1981), small and strap-shaped on highbush blueberry (Hodges et al 1979), attenuated and cupped on apple trees (Rom et al 1974), and distorted and stunted on other trees and vines (Lange and Schlesselman 1975). Clay (1972) stated that new leaves on treated apple trees elongated but remained narrow, the lamina failing to grow out.

From these observations, it appears that glyphosate moves from treated foliage to newly developing leaves, and also to storage organs in perennial plants from where it is sent to new growth in the following season. Its ability to affect plants in the season following application confirms the view that glyphosate can persist for some time within plant tissue.

(vii) Other effects:

Schumacher et al (1980) studied the effects of field applications of glyphosate on the seed morphology, germination and seedling establishment in C. arvense applied at the bud, flowering (soft dough) and late flowering (hard dough) stages. No achenes developed on plants treated at the bud stage while at the other two stages germination and seedling establishment were significantly reduced. Application at the "soft dough" stage resulted in the greatest decrease in seed weights and subsequent germination and emergence.

Leaf abscission has been noted with apple (Clay 1972), Citrus spp (Tucker 1977), and grape (Lee and Cahoon 1981); curling and twisting of the treated leaves on blackcurrant (Ribes nigrum) (Clay 1972), apple (Rom et al 1974) and grape (Lee and Cahoon 1981); a reduction in the silica content of the leaves in A. repens (Coupland and Casely 1975); production of tubers in the leaf axils of potato (Lutman 1979); and an increase in the gum exudation in peach (Prunus persica) (Rom et al 1976) and citrus (Tucker 1977) trees. Flowering in the season following treatment was delayed in blackcurrant (Clay 1972) and highbush blueberry (Hodges et al 1979), and the blueberry flower corollas became elongated.

(b) Translocation Studies Using Symptom Expression:

Most translocation studies with glyphosate have been conducted using 14-C-labelled material. Although this is a versatile technique which can give precise results, it has a number of drawbacks. It requires expensive equipment and it is usually only practical to sample a few plants. There is often some difficulty with interpretation of results, with one problem being that the presence of label in a tissue does not always mean that the tissue is being affected. Another technique for studying herbicide movement is the use of symptom expression by the treated plant. The use of this technique is illustrated in the following five examples. Note that the results obtained in these experiments are generally of practical significance because they show

how plants are affected by glyphosate rather than simply where it accumulates.

(i) Lee and Cahoon (1981):

Lee and Cahoon applied glyphosate to apical, sub-apical, penultimate or basal leaves of grape vines in a glasshouse. Movement out of the treated regions was measured by observing leaf damage and by calculating reductions in root growth. Many leaves located above the treated sub-apical region developed symptoms of damage, as did most of the terminal leaves with all treatments. Treatment in the penultimate region caused the greatest decrease in root growth although whether this indicated greater herbicide translocation or interference with carbohydrate translocation could not be determined.

(ii) Fernandez and Bayer (1977):

This experiment is similar to (i) above in that glyphosate was applied to various regions of Cynodon dactylon plants in a glasshouse, and movement was gauged by observing changes in colour and morphology. The regions treated were the rhizome tips, leaves attached directly to the rhizome, rooted tillers, tillers without roots, internodes, and tillers from the parent rootstock. The patterns of symptoms which developed led the authors to conclude that actively growing immature leaves at the stolon tips behave as strong sinks for glyphosate.

(iii) Rioux, Bandeen and Anderson (1974):

Rioux et al studied the speed of glyphosate translocation out of the treated leaves of Agropyron repens in a growth room by cutting them off 0, 1, 2 or 3 days after application and measuring the regrowth height, shoot number and fresh weight after 30 days. They concluded that glyphosate, or a toxic metabolite, moved in sufficient quantity during the first day to have a significant effect on regrowth and in 2 days to affect the regenerative potential of the rhizomes.

They also investigated movement into and out of the tillers at various growth stages by treating one tiller on a plant consisting of two tillers connected by a rhizome, and counting the number of leaves produced by the other tiller in the following 2 weeks. They found that leaf growth on the untreated shoot was inhibited at the 2- but not at the 4-leaf stage. They also found that glyphosate moved from the mother shoot to neighbouring tillers, but not vice versa, an indication of

phloem mobility.

(iv) Claus and Behrens (1976):

Claus and Behrens applied glyphosate to the leaves of A. repens plants with varying lengths of rhizome, and measured the extent of bud kill along the rhizomes in a glasshouse experiment. Rhizome buds on plants wth 20-90 nodes had a higher survival rate than those on plants with 10 nodes. When all buds were not killed, the survivors were mostly those closest to the mother shoot. This suggested preferential accumulation in the buds near the rhizome tip, an effect confirmed in experiments using 14-C-labelled herbicide.

(v) Lutman (1979):

Lutman was interested in the possibility of treating volunteer potatoes with glyphosate in low-growing crops using a ropewick applicator, and studied movement from the upper leaves into the rest of the plant. He compared treatment of one stem with treatment of all the stems arising from a tuber, using two tuber sizes and three concentrations. In another experiment he compared translocation from a stem sprayed along its entire length with that from stems sprayed or treated with a gel formulation at the top only. This was done in each case to one, all except one, or all of the stems of each plant. The plants were grown in pots but kept outside.

Lutman used a scoring system on a 0 to 6 scale to assess damage to untreated stems just prior to harvest. The scale had the following key points: 0 = healthy (as controls); 1 = growth of axillary buds; 2 = growth of axillary buds, death of stem apex, some chlorosis; 4 = death of stem apex and younger leaves, wilting and necrosis of older leaves; 6 = dead. This scoring system shows how some symptoms appear at lower concentrations than others. He also measured the weight of untreated stems, and the number of healthy and deformed tubers formed.

All doses applied to the top two to three leaves killed the stems below and the symptoms appeared more quickly with the higher than the lower concentrations. Most of the treated stems failed to initiate tubers, and of the few tubers that were produced, most were deformed with greatly reduced viability. However, the stems that were left untreated, although showing damage symptoms, were not killed and many plants were able to produce healthy tubers.

(7) SEXUAL DIMORPHISM IN CIRSIUM ARVENSE:

Some field observations have suggested that male C. arvense plants are more susceptible to glyphosate than female plants (R.W. Moore, pers comm). No support for this view has been found in the literature as regards glyphosate or other herbicides. One of the few studies on sexual differences in C. arvense is that by Lloyd and Myall (1976) who collected 50 pairs of male and female flowering stems and looked for morphological differences. On average, the male stems had significantly more ($P<0.05$) flower heads (24.3/stem) than the females (18.3/stem), although they were at similar stages of development late in the flowering season. The female heads were described as differing in appearance from the male heads due to differences in size of involucres, florets and pappus. No pollen was observed to be produced by the female flowers, although occasional achenes were produced by the males.

Extensive vegetative reproduction often makes the individual genotype limits uncertain, so that the sex ratio is difficult to determine accurately. Lloyd and Myall counted stems at intervals along transects and calculated an overall proportion of 47% females, which did not differ significantly from equality. Cassini (1823) and Correns (1916) also noted an approximate equality of the sexes, although Bakker (1960) observed that "male and female plants occur in the ratio of about one to three" in the Netherlands.

METHODS AND MATERIALS

(1) PROPAGATION METHODS:

Seeds were collected in the autumn of 1981 from the heads of senescent C. arvense plants growing in a paddock beside Tiritea Road, Palmerston North. They were placed in petri dishes on germination blotters moistened with 0.1% potassium nitrate solution on 26th August 1981, and germinated under illumination at a constant temperature of 30 C. Of the 600 seeds used, 62% germinated 6 to 20 days later. Seedlings were planted into individual 180 ml waxed paper cups containing a potting mixture of equal parts peat, sand and perlite approximately 24 hr after germination. The cups were placed in a glasshouse with the thermostat set at minimum and maximum temperatures of 18 and 22 C respectively. Hygrothermographs recorded fluctuations in temperature and relative humidity. The seedlings were watered when necessary and given 10 ml of nutrient solution once a week.

The healthiest seedlings were transplanted into No 10 Planta Bags (140 x 140 x 420 mm) during the second week of October, at which time they had five to seven leaves and a tap-fibrous root system 15-20 cm long (see Plates 1 and 2). The potting mixture used was the same as above, but a fertilizer mix was added consisting of 240 g dolomite, 192 g long term "Osmocote" (a controlled release fertilizer), 48 g short term "Osmocote", and 12 g of fritted trace elements per 80 l of potting mix. The bags were initially kept on trolleys covered in sheets of plastic and felt so that water could be trapped around the bases of the bags, keeping the soil in the bags moist (see Plate 3). When the plants grew larger, they were placed on felt mats on the floor of the glasshouse with soak hoses passing under the mats to keep them damp (see Plate 4). The plants occasionally suffered slight water stress, apparently due to a halt in the upward movement of water through the soil, and this was overcome by watering the tops of bags at these times.

The plants were attacked by a number of pests, notably mites, white-fly and aphids. The glasshouse was periodically fumigated with dichlorvos, and the systemic insecticide acephate was also used. A fungal disease which occasionally infected the plants was controlled using zineb.

PLATE 1: The 5-week-old seedlings immediately prior to transplanting into bags. (9th October)

PLATE 2: The extent of root development in seedlings 5 weeks after germination. (9th October)

PLATE 3: The bags were kept on wet felt mats on trolleys while the plants were young. The white paper around the bags helped minimize heating of the bags by the sun. (24th October)

PLATE 4: The plants were put on felt mats on the floor once they grew larger, and soak hoses ran under the mats. (11th November)

(2) EXPERIMENTAL DESIGN:

Three separate experiments were conducted, in all of which the commercial form of glyphosate (360 g ai/l as the isopropylamine salt in the aqueous solution) was used at a dilution of two parts water to one part glyphosate, the concentration recommended for use in ropewick applicators (Monsanto 1982). All experiments were replicated five times and arranged in a completely randomised design.

(a) Growth Stage Experiment:

Plants in this experiment were treated when the mother stem was at one of five growth stages:

(i) Vegetative stage:

The mother stem had elongated enough to allow treatment with a ropewick applicator, but no buds had formed. Characteristics of plants at this and the other four growth stages appear in Table I. Although an average of 46% of the nodes had axillary growth at this stage, only 30% of axillary shoots were longer than 1 cm.

(ii) Early bud stage:

Flower buds had formed on mother stems treated at this stage but the axillary stems were still short so that the buds were crowded at the stem apex (see Plate 5). Elongation of the main stem was still occurring.

(iii) Late bud stage:

Elongation of the main stem and uppermost branches was complete, and the first flowers were about to open.

(iv) Flowering stage:

Three stages of flower development have been distinguished. Young - in which the involucres were green and the florets with full colour, old - in which the florets had lost their colour and the involucres were still closed and green, and senescent - with necrotic involucres which had opened and necrotic pedicels. Plates 6 to 8 show male and female flowers at these three stages of development.

TABLE I: Characteristics at time of treatment of plants used in the Growth Stage Experiment. Values are means of measurements made on the mother stem, unless otherwise stated. Figures in parentheses are ranges of the values. See Appendix 1 for a full set of measurements.

Parameter	Growth Stage				
	Vegetat.	E. bud	L. bud	Flow.	Post-fl.
Treatment time	early Dec	mid Dec	early Jan	mid Jan	early Feb
Height (cm)	50.5 (30-71)	99.4 (73-120)	149.0 (96-181)	141.7 (101-174)	150.8 (111-171)
No. of nodes	26.2 (20-31)	39.7 (33-49)	45.6 (37-55)	40.6 (32-49)	40.5 (36-54)
% of nodes with axillary growth	47.6 (0-77)	82.4 (36-98)	91.5 (49-100)	-	-
No. of flower buds	0	25.4 (10-54)	68.8 (13-153)	53.4 (13-116)	7.8 (0-32)
No. of flowers	0	0	0	29.2 (12-59)	69.9 (30-113)
No. of daughter stems > 20 cm	4.7 (0-13)	5.1 (1-11)	6.5 (2-15)	7.8 (3-14)	8.6 (3-19)

PLATE 5: A stem at the early bud stage.

PLATE 6: Male flowers and buds. From left to right the flowers would be termed old, young, senescent, old and young.

PLATE 7: Female flowers and buds. The centre flower would be termed old and the other two as young.

PLATE 8: Senescent female flowers.

The average mother stem treated at the flowering stage had 14.2 old flowers, 15.4 young flowers, 53.4 buds and almost no senescent flowers. The older flowers tended to be those on the uppermost branches and those nearest branch tips. An average of 10.4 branches per stem bore flowers or buds (8.4 had flowers). The lower branches were generally very short and without buds or flowers.

(v) Post-flowering stage:

The average mother stem of plants treated at this stage had 23.8 senescent, 39.2 old and 6.9 young flowers and 7.8 buds. On many plants a few buds and flowers were still developing on lower branches.

For each growth stage, glyphosate was applied to the mother stem at rates of 0, 1.5, 6.2, 25 or 100 mg ai/stem. The 1.5 and 6.2 mg treatments were applied using a micropipette to the upper surfaces of 1-6 main stem leaves approximately 5-15 cm from the apex. These leaves were still expanding in earlier growth stages but were fully developed in later growth stages, and were treated because of being positioned where a ropewick applicator is most likely to strike. The 25 and 100 mg treatments were applied with a No 2 artists paint brush to as many of the upper leaves as was required to use up the appropriate volume of herbicide solution. The 100 mg treatment involved application of 0.833 ml of herbicide solution which often meant that most of the leaves on the mother stem had to be treated.

(b) Plant Part Experiment:

The second experiment compared the effectiveness of glyphosate when applied to different parts of the mother stem. Treatments consisted of 25 mg ai of glyphosate (0.208 ml solution) applied with a paint brush to the stem and leaf tissue in the (i) upper, (ii) middle, or (iii) lower thirds of the stem; or to (iv) leaves of axillary branches, (v) the stem, (vi) the flower buds, or (vii) the leaves on one side of the main stem only. These plants were compared with (viii) untreated plants, and (ix) plants with all parts of the mother stem treated.

At treatment the first flowers were just opening on the mother stems, ie the development stage was between the late bud and flowering stages used in the first experiment. The average mother stem was 148.2 cm tall, had 40.8 nodes, 94.7% with axillary growth, and had 77.4 buds, 6.4 flowers

and 6.1 daughter stems taller than 20 cm (Appendix 1.6).

(c) Leaf Side Experiment:

Another small experiment was conducted to compare the effectiveness of glyphosate applied to the upper and lower leaf surfaces of C. arvense using a dose of 25 mg. The plants were treated at a stage slightly earlier than that in the plant part experiment. The average mother stem was 141.9 cm tall, had 37.8 nodes, 93.6% with axillary growth, and had 94.6 buds, 4.1 flowers and 5.7 daughter stems taller than 20 cm (Appendix 1.7).

(3) MEASUREMENTS AND OBSERVATIONS:

Measurements and observations were made of plants at five different times during the experimental period.

(a) At Treatment:

Immediately prior to treatment, the following parameters were measured on the mother stem and two largest daughter stems of each plant: height, number of nodes, number of branches at particular stages of development (eg shorter than 1 cm, with flowers), and the numbers of buds and flowers at particular stages of development. A coloured tag was put on each of these stems to distinguish them later and the number of daughter stems was recorded.

(b) One Week After Treatment:

A spot of paint was put near the top of each of the three stems 1 week after treatment, and the distance from the paint spot to the stem apex was measured. The measurement was repeated 3 days later to determine if stem elongation was still occurring. Actively growing leaves or branches were also marked on each of these stems so that their growth could be measured, and visual symptoms were noted.

(c) Four Weeks After Treatment:

Measurements of the marked plant parts were repeated 4 weeks after treatment, and further notes made of visual symptoms.

(d) Main Harvest:

Approximately 3 months after treatment, all stems of each plant were cut off at the base, leaving the roots undisturbed. Every stem with a tag and/or with buds or flowers was individually weighed immediately after being cut and the following parameters measured: height; number of nodes, green leaves on the main stem, and buds and flowers at various stages of development; the length of the longest branch; and the maximum diameter of the main stem. With the tagged stems, measurements were also made of the parts marked for growth studies, and the number of branches at particular stages of development. The state of health and presence or absence of glyphosate-induced damage were noted for every stem. Individual heights and the overall weight of vegetative, untagged stems were recorded. All stems were then dried for 24 hr at 80 C and weighed again to determine dry weights and dry matter percentages.

The bags were put back in the glasshouse to allow regrowth of the roots to occur.

(e) Second Harvest:

The numbers, fresh and dry weights and dry matter percentages of regrowth shoots were recorded 21 days after the main harvest. The roots were removed from the soil and a stream of pressurized air used to clean off the soil. Their condition was noted, and fresh and dry weights determined.

RESULTS

(1) MEASURES OF GLYPHOSATE EFFECTIVENESS:

As several types of measurement were made of plants during the trial, it was necessary to select which parameter gave the best measure of control effectiveness of C. arvense by glyphosate. The herbicide caused foliar necrosis, and thus an increase in dry matter percentage of stems. It caused distinctive forms of damage to the plants, the type and intensity of which varied with rate of application. It also affected regrowth and caused decomposition of the root system (Appendix 2).

(a) Necrosis:

A highly significant increase in the average dry matter percentage of plant stems was measured at the main harvest as the treatment rate was increased (Appendix 3.1). ("Significant" = significant at the 5% level of probability; "highly significant" = significant at the 1% level of probability.) However, Fig 3 shows that dry matter percentages were also larger due to natural senescence for harvest dates later in the season, making this parameter unsuitable for comparisons between plants harvested at different times.

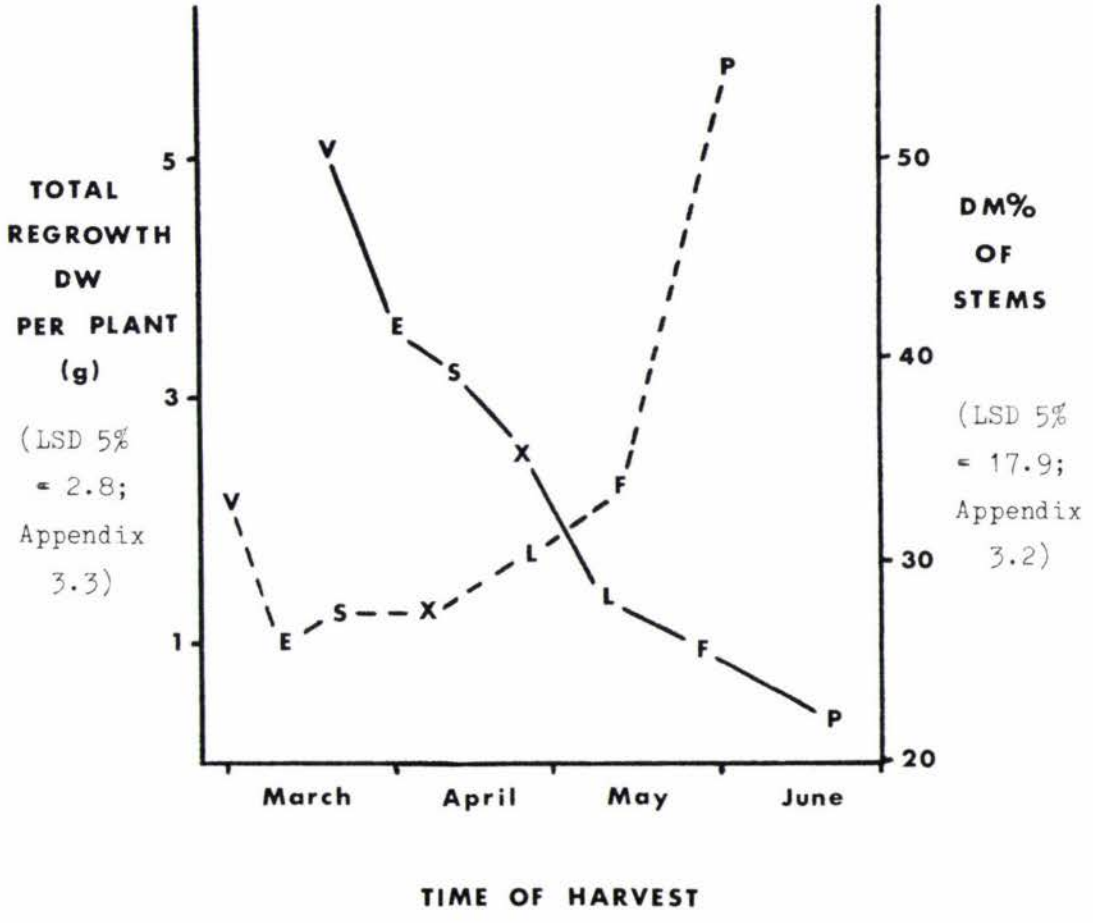
(b) Scoring of Damage:

Because plants harvested late in autumn were mostly necrotic due to senescence it was very difficult to use a scoring system for damage as the necrosis disguised many of the characteristic damage symptoms. Scoring was also made difficult due to plants treated when young being affected differently from those treated when more mature so that comparisons of scores between different growth stages would have been misleading. In addition, both stem dry weight percentage and symptom expression are measures of short term effectiveness of glyphosate on C. arvense, giving no real indication of whether the plant would recover in the following season.

(c) Regrowth:

The regrowth of plants during the 3 weeks after removal of the above-ground parts also gave a poor indication of long term control. Less regrowth was produced by control plants late in autumn (Fig 3) due to decreases in both the number of regrowth stems per plant and the

FIGURE 3: Average regrowth dry weight (solid line) and stem dry matter percentage (broken line) of untreated plants from vegetative (V), early bud (E), late bud (L), flowering (F) and post-flowering (P) growth stage treatments, and Leaf Side (S) and Plant Part (X) Experiments, plotted against times of harvest. Each point is the mean of five replicates.



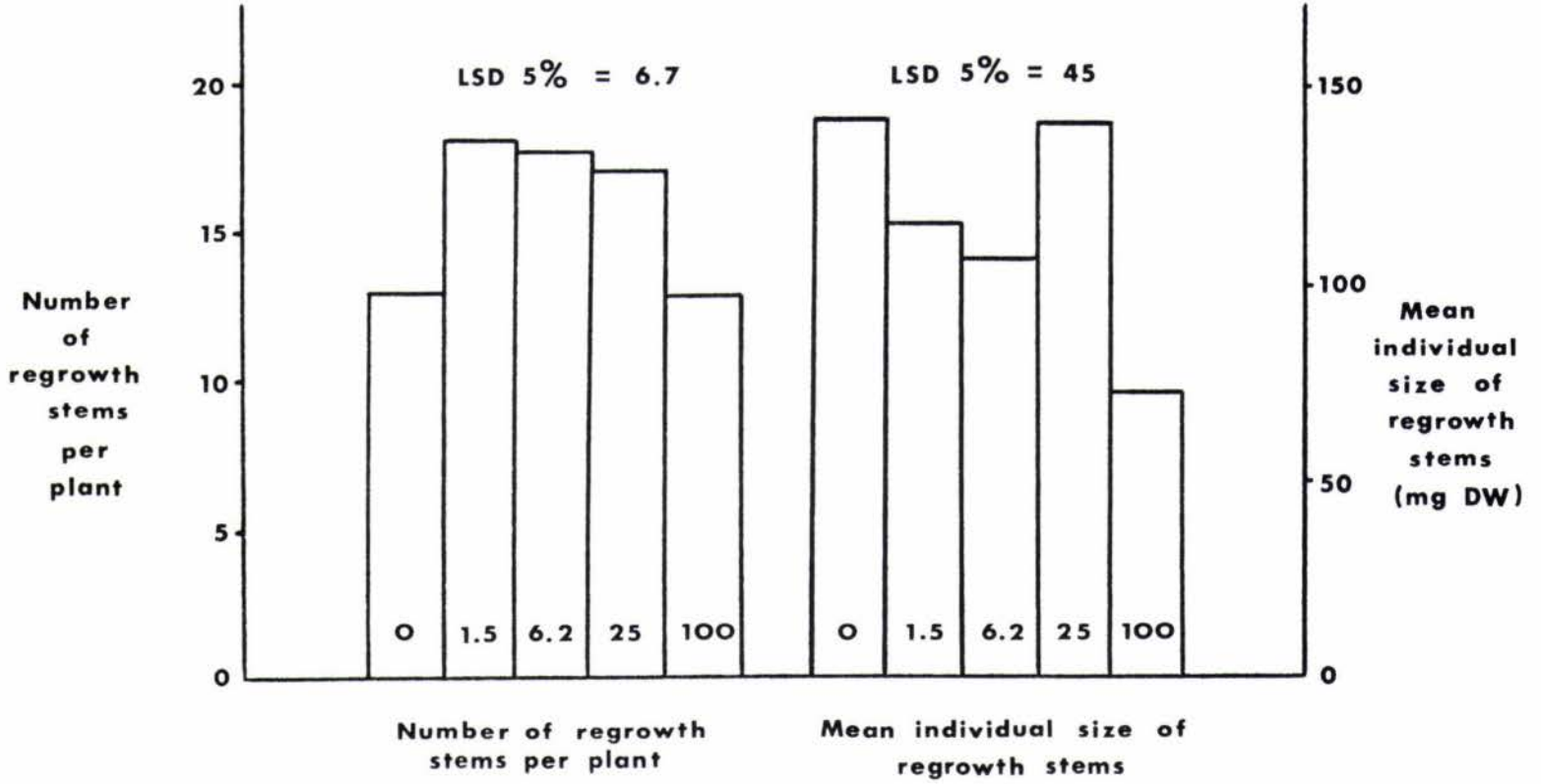
average weight of individual stems. Another problem was that the relationship between application rate and regrowth after cutting was not a simple one. Fig 4 shows that the lower rates of glyphosate tended to increase the number of regrowth shoots produced after the main harvest, though these increases were not significant statistically (Appendix 3.4). Regrowth from treated plants was generally smaller than that from the controls, though the difference was only significant at the 100 mg rate (Appendix 3.5). As a result, total regrowth dry weight produced per plant was similar for controls and treatments up to 25 mg of glyphosate, while there was an appreciable (though not significant) decrease in regrowth produced with the 100 mg treatment (Appendix 3.6). Variation in results was large and untreated control plants with healthy roots failed to produce regrowth in some cases while, in others, root systems which were completely necrotic did have regrowth.

(d) Root Decomposition:

The plants which were worst affected had almost no root material left after 3 months due to extensive decomposition (Appendix 2). Such plants would obviously be the least likely to reestablish successfully in the following season, so it was decided to use a measure of root decomposition to gauge the effectiveness of glyphosate in controlling C. arvense. Because of the great variation in plant size, the shoot:root ratio was calculated in an attempt to distinguish between low root weights caused by glyphosate action and the naturally low root weights of small plants. In small plants the ratio was similar to that for large plants, while plants badly affected by glyphosate underwent extensive root decomposition in the moist soil while the stems simply dried out and lost very little dry weight.

As the roots were weighed after the 3 week regrowth period, the weight of the rhizome material from the regrowth was included in this measurement. This material sometimes comprised an appreciable proportion of the total weight and so the regrowth shoot weight was added to the shoot weight recorded at the first harvest for the shoot:root ratio calculations (ie S:R ratio = [stem DW + regrowth DW]/root DW). The shoot:root ratio data violated two assumptions used in the analysis of variance by not being normally distributed and having different variances. So the data was log transformed (logarithms to the base 10) as the resulting data complied with both of these requirements. Untreated plants generally had shoot:root ratios below 8 (log ratio =

FIGURE 4: Average regrowth characteristics following stem removal of plants treated with glyphosate at 0, 1.5, 6.2, 25 or 100 mg/plant.



0.9), while necrosis was fairly extensive in plants with ratios exceeding 10 (log ratio = 1.0) and ratios above 30 (log ratio = 1.5) occurred when the roots had almost entirely rotted away.

As occurred with dry matter percentage and regrowth, log shoot:root ratios of control plants varied with time of harvest (Fig 5). The significant decrease in the ratio between March and June was due to an increase in root dry weights while the stem dry weights remained fairly constant (Fig 6). Thus little importance was attached to variations in log shoot:root ratios for values below 1.0.

Unfortunately extensive root decomposition only occurred in about 15% of the treated plants because of the low rates of glyphosate used. In the Plant Parts and Leaf Side Experiments there was very little root breakdown and the differences between log shoot:root ratios for the treatments in these two experiments were not significant statistically (Appendices 3.10 and 3.11). However the differences between root dry weights were significant in the Plant Parts Experiment (Appendices 3.12 and 3.13). Root and stem growth were both greatly reduced even by low doses of glyphosate, but as both were affected to approximately the same extent, the ratio was little affected.

A reduction in root growth does not necessarily mean that glyphosate was acting within the roots and could be an indirect effect caused by reduced shoot growth. Root decomposition is a more positive indication of the presence of glyphosate (though the possibility of indirect effects can still not be entirely discounted) and it was the treatments resulting in translocation to the roots which were mainly of interest. Thus even though the differences between the log shoot:root ratios in the Plant Parts Experiment were not significant, this parameter will be used to illustrate the apparent trends in translocation. The relationships between the treatments were very similar for the log shoot:root ratios and the root dry weights and use of the former makes comparisons with the Growth Stage Experiment possible.

In the Leaf Side Experiment it was considered more important to compare differences in uptake than to assess translocation so that measurement of the effects on shoot and root dry weights were sufficient.

FIGURE 5: Average log shoot:root ratios of untreated control plants from vegetative (V), early bud (E), late bud (L), flowering (F) and post-flowering (P) growth stage treatments, and Leaf Side (S) and Plant Part (X) Experiments, plotted against times of harvest. See Appendix 3.7 for analysis of variance.

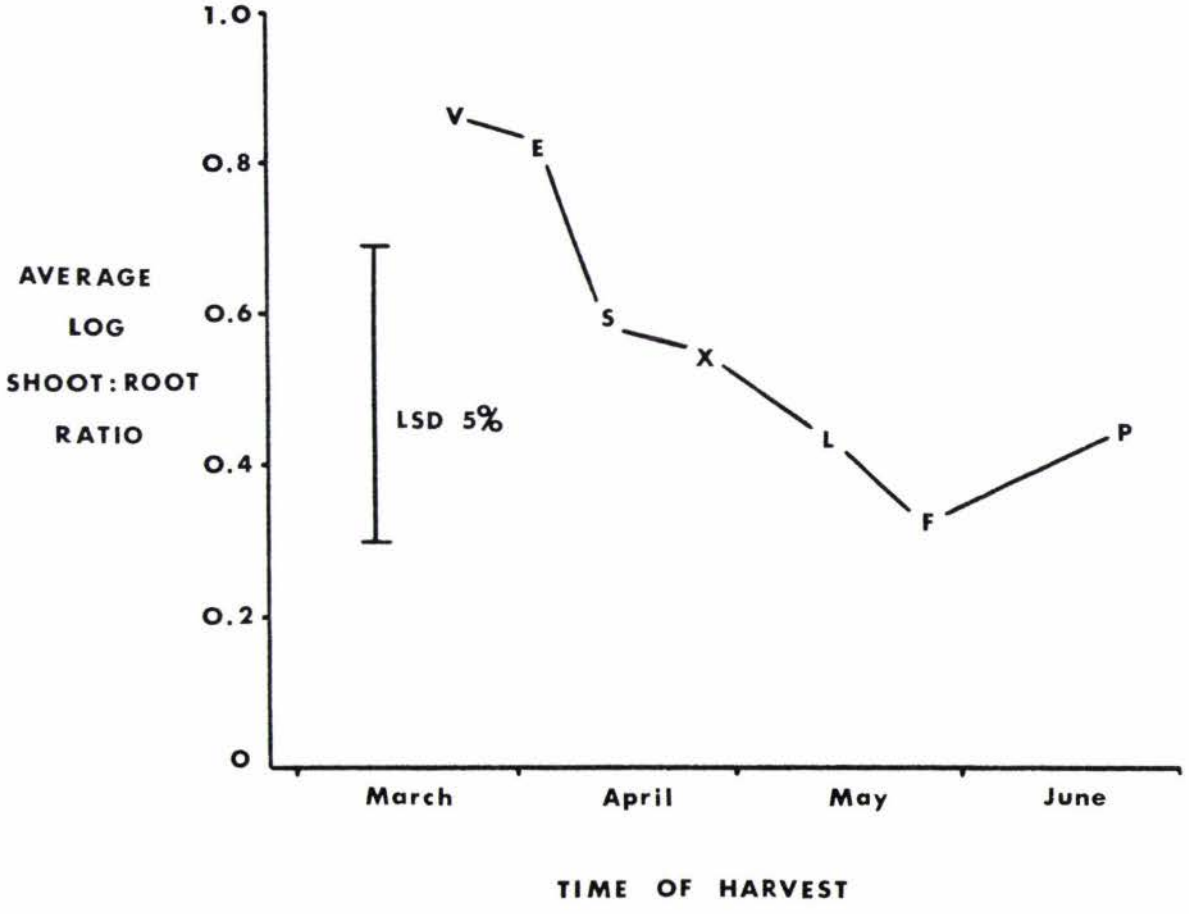
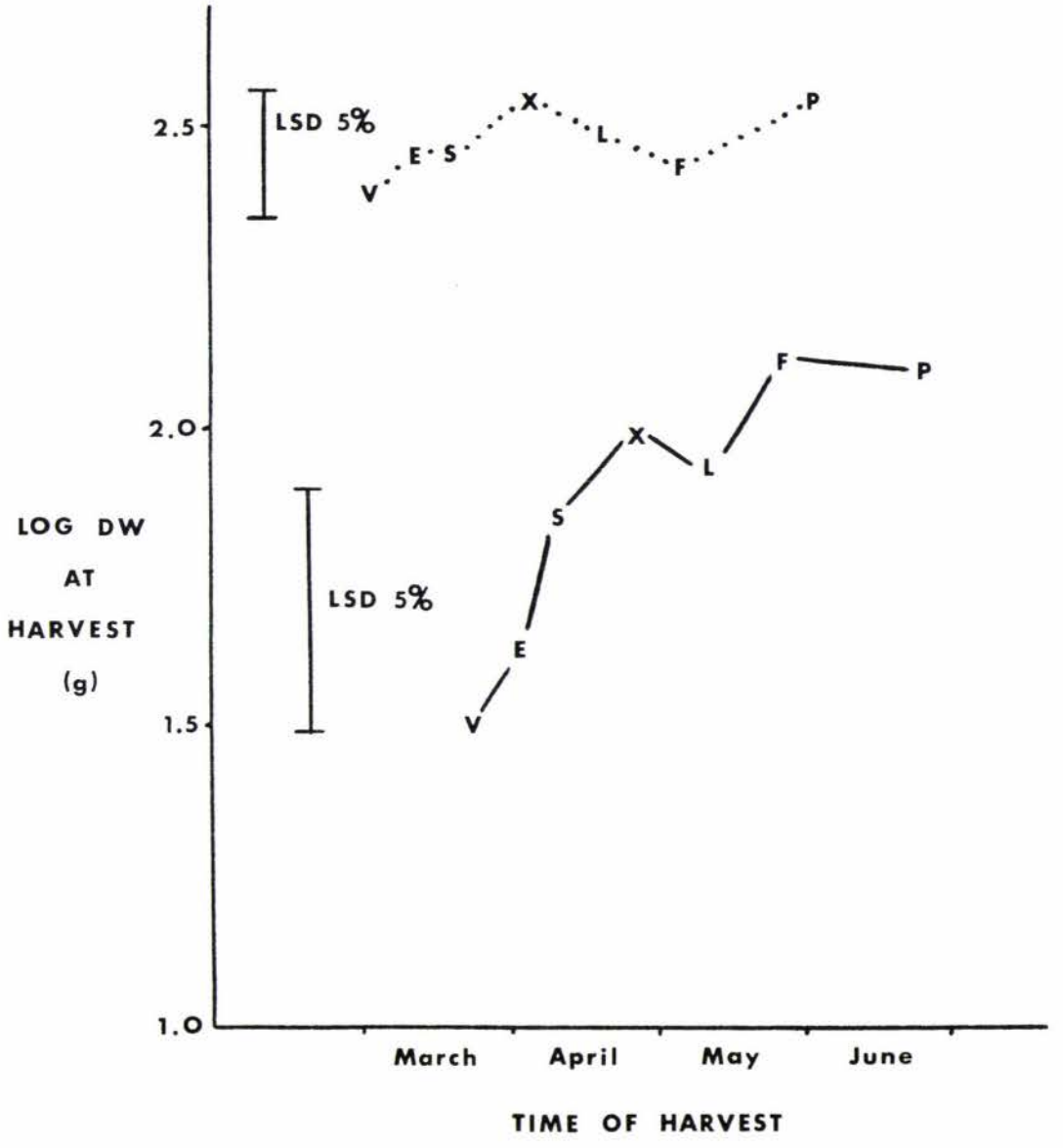


FIGURE 6: Average log shoot dry weight (dotted line) and log root dry weight (solid line) of untreated plants from vegetative (V), early bud (E), late bud (L), flowering (F) and post-flowering (P) growth stage treatments, and Leaf Side (S) and Plant Part (X) Experiments, plotted against times of harvest. See Appendices 3.8 and 3.9 for analyses of variance.



(2) GROWTH STAGE EXPERIMENT:

(a) Symptoms:

Glyphosate caused the development of a variety of symptoms on C. arvense plants, the type and intensity of which varied with rate of application and plant maturity at time of treatment.

(i) Necrosis after 1 week:

Necrosis was a common symptom. Treated leaves were usually partially to completely necrotic 1 week after treatment and the effect tended to be very much of a contact nature at this stage. If a leaf was only partially covered in glyphosate, only the treated parts would be necrotic after 1 week, while the untreated parts would remain a healthy green colour, even if the untreated part was only one lobe of the leaf. Glyphosate smeared on to a leaf from the tip of a micropipette often caused a necrotic zig-zag design on the otherwise green surface 1 week after treatment. (Note that the leaf surface was never broken during treatment.) All parts of treated leaves generally became necrotic during the following weeks, but often the last parts to be affected were those next to midribs and the main leaf veins (Plates 9 and 10).

If stem tissue was treated, there tended to be only a brownish discolouration of the surface after 1 week rather than necrosis of the tissue, though a few necrotic lesions sometimes appeared. C. arvense stems have light-coloured vertical ridges which extend downward from the petioles (Plate 11), and microscopic examination of these ridges showed each ridge to contain a vascular bundle. At the higher rates of application, these ridges were often necrotic in the vicinity of treated leaves 1 week after treatment (see Plate 12).

(ii) Chlorosis:

Other than necrosis of the treated leaves, the most common symptom found 1 week after application was yellowing of developing leaves both on the treated mother stem and the associated daughter stems. (At low rates of application, less yellowing of daughter stems occurred.) When stems were at a vegetative stage of growth, the newly developing apical leaves were affected (Plate 13). At later stages of development, the effect was more evident on the young axillary leaves (Plate 14). The intensity of yellowing varied between stems and also between the leaves in the

PLATE 9: A treated leaf in the process of turning necrotic. Note the healthy tissue beside the midrib and major veins.

PLATE 10: Treated leaves which have turned completely necrotic.

PLATE 11: A stem of an untreated *C. arvense* plant, showing the light-coloured ridges.

PLATE 12: Necrosis of ridges on the stem of a treated plant.

PLATE 13: Apical leaves of a vegetative mother stem yellowing 1 week after glyphosate application to the partially necrotic leaf shown in the bottom right-hand corner.

PLATE 14: The stem on the left was treated with glyphosate, resulting in chlorosis of apical and axillary leaves of associated daughter stems.

affected area of one stem, with the youngest being more affected than older leaves. Leaves which were larger than about a third of their final size when treated were never affected by this yellowing. On many leaves which developed only slight yellowing there was also a green net-like pattern resulting from the tissue beside the major veins remaining green while the rest of the leaf turned yellow (Plate 15). The leaf tips and the tips of the lobes often also remained green in such leaves (Plate 16). Badly affected leaves were completely yellow and often had numerous tiny necrotic specks dotted over the surface.

In stems receiving higher rates of glyphosate, small necrotic lesions were sometimes found 1 week after treatment on the larger, more mature leaves which were not yellow, particularly those on the upper part of the stem.

(iii) Growth:

Stems which were treated at growth stages when elongation was still occurring generally suffered severe reductions in extension growth at the lowest rate of application, and total inhibition at higher rates. Axillary stem growth was likewise affected, though higher rates were required before expansion of leaves on the treated stem and elongation of daughter stems were affected. Generally only leaves with severe yellowing or necrosis stopped growing during the first few weeks after treatment.

(iv) Symptoms after 4 weeks:

Four weeks after treatment, tissues in the top part of treated stems were mainly necrotic, though this was not always the case with lower rates. Stems on which only a few leaves were treated (low rates) were often necrotic only in regions where growth was active at the time of treatment, while stems receiving higher rates tended to be completely necrotic in all parts above the lowest point of application. Often there was a sharp transition from healthy to necrotic tissue coinciding almost precisely with the lowest point of application, which was marked by a tag loosely tied around the stem (Plate 17).

Leaves on daughter stems which were yellow after 1 week were necrotic after 4 weeks on the more severely affected plants. In those daughter stems affected at a vegetative growth stage all tissues in the top portion of the stem were often necrotic by the time of the main harvest.

PLATE 15: The green net-like design that formed on less affected leaves. Note the green tissue beside major veins.

PLATE 16: An affected leaf (right) several weeks after treatment beside an unaffected leaf. Note the green tips of lobes.

PLATE 17: Necrosis of the treated portion of a stem several months after treatment. Black wool tied around the stem just above the green leaves marks the lowest point of application. The leaves at the bottom of the stem are displaying normal senescence.

PLATE 18: Some distorted leaves showing the reduction in size and number of spines. The leaf on the far right is normal.

On these stems there was often a sharp transition from healthy to necrotic tissue. The necrotic leaves and stem remained the same size as when first affected, or withered somewhat, whereas those immediately below continued growth totally unaffected. This resulted in the development of stems of normal diameter with normal leaves above which was an area of necrotic tissue much smaller in size relative to the healthy tissues.

Leaves on the daughter stems which had shown less effect at 1 week showed various forms of distortion 4 weeks after application. In the commonest distortion the leaves became strap-like in appearance, apparently through a continuation of elongation combined with a cessation of lateral expansion. A common feature of leaves which became distorted, no matter to what extent, was a reduction in the size and number of spines, with a complete absence of spines in some cases (Plate 18). Leaves which were yellow 1 week after treatment but did not become necrotic were generally bleached by 4 weeks in addition to being distorted (Plate 19).

The extent to which vegetative daughter stems were affected by treatments applied to the mother stems varied. In some cases, all apical leaves became necrotic, preventing further growth in height. In others the apical leaves did not die but remained distorted, similar to the leaves shown in Plate 19, with very little further growth in height. However, in less affected stems, apical growth, although distorted, continued with the eventual production of normal leaves. At the main harvest, these stems had a distinctive appearance in which the leaves at the bottom and the top of the stem were normal, while an intermediate section bore leaves which were small and distorted. Such leaves were often either bleached or necrotic and situated close together due to the short length of the internodes (Plate 20).

(v) Axillary growth:

A common feature of affected stems, whether the treated mother stem or untreated daughters, was the growth of several long axillary branches after apical growth had been restricted or stopped (Plate 21). These stems were sometimes longer than the main stem and were equally likely to grow from any of the nodes below the affected area. Often the first leaves on the axillary stems were distorted, but the later leaves progressively approached normal with the production of healthy flowers

PLATE 19: Typical bleached strap-like growth of young apical leaves affected by glyphosate.

PLATE 20: From left to right are leaves taken from top to bottom from the affected portion of a stem which recovered from a dose of glyphosate.

PLATE 21: A daughter stem affected by glyphosate. Internodes are short and leaves distorted on the upper portion of the main stem, and long axillary stems have formed with distorted leaves near their bases.

PLATE 22: Distortion of C. arvense buds and flowers by glyphosate.

at the apices. Many of the apical meristems of the main stems bearing these long branches were obviously inactive and necrotic. In some cases however, distorted apical growth was still occurring.

(vi) Flowers:

Flower buds on treated stems generally showed no sign of glyphosate damage 1 week after glyphosate application, but were usually completely necrotic after 4 weeks, along with surrounding leaves and stems. The larger necrotic buds often eventually opened but contained no florets. Less affected buds on mother and daughter stems which were well developed at the time of treatment often remained green and commenced flowering. In some cases, the buds did not open properly, trapping the florets inside. If they did open fully, the florets that emerged were often distorted and sometimes white or brown. Usually these florets did not mature and the involucres were twisted in appearance. Buds which were small at the time of treatment, or which developed later on more affected stems, usually became distorted and twisted. They generally remained small in size, had a waxy appearance and were often bleached (see Plate 22). They seldom opened.

The effect of glyphosate on flowers depended on the developmental stage at the time of treatment. Flowers which had just opened or were opening when the stem was treated usually suffered discolouration of the florets soon after treatment, becoming off-white and then dark brown (Plate 23). The involucre often twisted, and later became prematurely necrotic. These flowers usually showed no signs of achene development and had an abnormal appearance (Plate 24). Flowers which had been open for a few days before treatment generally appeared to develop achenes successfully, though it is not known whether they would have been viable. Very few seeds developed fully on any plants as pollinating insects were not present in the glasshouse. Seeds in healthy unpollinated flowers were the same length as viable seeds but were shrivelled rather than plump. Flowers on daughter stems were usually not affected much by glyphosate applied to mother stems, though distortion and discolouration sometimes occurred.

On a number of male plants, flowers on daughter stems which were otherwise hardly affected by glyphosate took on the appearance of female flowers. As can be seen in Plates 6 and 7, female flower heads look distinctly different from males, and the differences have been described

PLATE 23: Glyphosate-induced browning of female florets.

PLATE 24: Distortion of male flowers as seen at the main harvest. The flowers on the far right are normal.

in detail by Lloyd and Myall (1976). On male plants where this apparent reversal of sex occurred, flowers were present which looked exactly like those shown in Plates 7 and 8, though whether these flowers were functional females was not determined. These flowers were buds when glyphosate was applied. Flowers resembling males were never seen to form on treated female plants.

(vii) Natural senescence:

Whereas necrosis could be used as an indication of glyphosate damage at the main harvest of the first two growth stage treatments, necrosis due to senescence was common in plants of the three stages harvested later in autumn. Senescence generally involved yellowing of leaves followed by necrosis (Plate 25), but this yellowing was easily distinguished from that caused by glyphosate as the latter colouration was much paler than the former. Senescence occurred first in the lower third of a stem, then began at the apex and progressed downward. Senescence was just beginning in older stems when the post-flowering stage plants were treated.

(viii) Plant death:

The plants which were most severely affected died in a characteristic manner. They looked no different from other treated plants 1 week after treatment. However, at 4 weeks all stems of such plants looked severely water stressed. All leaves were flaccid. These leaves became necrotic after a few days, usually turning senescent yellow first. The leaves at the bottom of the stem generally died first and those at the apex last. The stem generally remained green for some time after the leaves had died, but eventually became necrotic as well. The yellow and brown colours of the leaves on plants which died rapidly were different from the normal glyphosate symptoms. It usually took only a week for all stems on a plant to die in this manner though the process did not begin until 3-4 weeks after treatment. On examination most of the roots of such plants were found to have decomposed, though often a few healthy sections remained. Regrowth developed from some of these sections both before and after the main harvest. This rapid death was seen in only 12 of the plants treated in the Growth Stage Experiment, all of which had received 100 mg of glyphosate, except for two plants treated at the vegetative stage with 25 mg. All five plants treated with 100 mg at the post-flowering, two at the vegetative, two at the flowering and one at the late bud stages of growth died in this manner. Another two plants

PLATE 25: Senescence of a C. arvense plant.

PLATE 26: Healthy regrowth 3 weeks after the main harvest.

PLATE 27: Slightly distorted regrowth 3 weeks after the main harvest.

PLATE 28: Severely distorted regrowth.

treated with 100 mg at the vegetative stage displayed these symptoms but survived. Most of the other plants gradually senesced over the months following treatment at approximately the same rate as untreated controls, and generally no further glyphosate-induced damage developed after 4 weeks.

(ix) Regrowth:

Regrowth of plants receiving the higher rates of glyphosate tended to be small and pale in colour, often with abnormally shaped leaves (Plates 26-28). A number of bags contained both abnormal and normal regrowth originating from different sections of root. When harvested, glyphosate-affected roots often had large numbers of thin, white, vertical rhizomes of recent origin, similar in appearance to the rhizomes of normal regrowth shoots, but only a few centimetres in length and with insufficient vigour to reach the soil surface.

(x) Overall effects:

Apart from the wilting phenomenon, stems treated at earlier stages of development were visibly more affected by glyphosate than more mature stems. Although the treated regions of stems often became extensively necrotic at all growth stages, those treated when young also usually suffered distortion and necrosis of the developing leaves, and made no further growth in height whereas stems treated when more mature often appeared little different from untreated plants at harvest apart from the presence of some distorted buds and flowers. Glyphosate affects growth processes, and it was the stems which had almost finished development when treated which were visibly least affected.

In the case of daughter stems, it often appeared that less glyphosate was translocated to the more mature stems anyway, so older daughter stems almost always looked less affected than younger ones.

Young vegetative daughter stems usually showed some sign of the effects of glyphosate, the higher doses generally affecting a greater proportion of the stems and having a greater effect on individual stems. However, on one plant it was common to find some daughter stems showing an effect while others apparently identical in size and growth stage were totally unaffected. Likewise, plants treated with the same amount of glyphosate at the same growth stage were often affected to very different degrees.

The entire plant seemed to be less affected by glyphosate when treated at later growth stages. Although this was partly due to the older plants having greater proportions of mature stems, even the young vegetative daughter stems in older plants tended to be less affected.

(b) Root Decomposition:

Table II shows the log transformed shoot:root ratios of the plants, with each value being the mean of five replicates. An F test showed a highly significant difference in log shoot:root ratios for the different herbicide rates (Appendix 3.14). Although the 1.5, 6.2 and 25 mg rates caused no significant increase in shoot:root ratio compared with the untreated control, the difference between the 100 mg and other treatments was highly significant. There were no significant overall differences between the five growth stages.

As the only plants to have their shoot:root ratios significantly affected by glyphosate were those treated with 100 mg, an analysis of variance of the log shoot:root ratios was done for just the plants treated with 100 mg (Table III) in case the plants treated with lower rates of glyphosate had disguised growth stage treatment effects in the analysis of Table II. However there were still no significant differences detected between the treatments (Appendix 3.15) and Table III shows how the results were particularly variable. As mentioned earlier, plants with log shoot:root ratios above 1.00 had appreciable amounts of root decay. Table III shows that two out of five plants had values above 1.00 for the vegetative, late bud and flowering treatment groups, whereas no plants exceeded 1.00 for the early bud group and all plants treated at the post-flowering stage were above this value. This suggests that C. arvense is most susceptible to glyphosate applied at the post-flowering growth stage and most tolerant to early bud application, even though such conclusions cannot be justified statistically.

The mother stems treated at the vegetative growth stage varied in maturity when treated. The percentage of nodes with axillary growth, a parameter which increased with maturity, varied from 0% to 77%. The less mature plants treated at this stage appeared more susceptible to glyphosate than the more mature plants, and this relationship has been shown in Fig 7. As might be expected from the fact that plants treated with smaller amounts were not affected regardless of maturity, the trend

TABLE II: The log shoot:root ratios of C. arvense plants treated with different doses of glyphosate at different stages of growth. See Appendix 3.14 for analysis of variance.

Application rate (mg/plant)	Growth stage at treatment					Mean
	Veget.	E. bud	L.bud	Flow.	Post-fl.	
0	0.86	0.83	0.44	0.31	0.45	0.58
1.5	0.58	0.70	0.60	0.42	0.46	0.55
6.2	0.64	0.68	0.65	0.44	0.49	0.58
25	0.68	0.70	0.36	0.51	0.62	0.57
100	1.07	0.48	0.94	1.06	1.37	0.99
Mean	0.77	0.68	0.60	0.55	0.68	0.65

LSD 5% (means) = 0.21

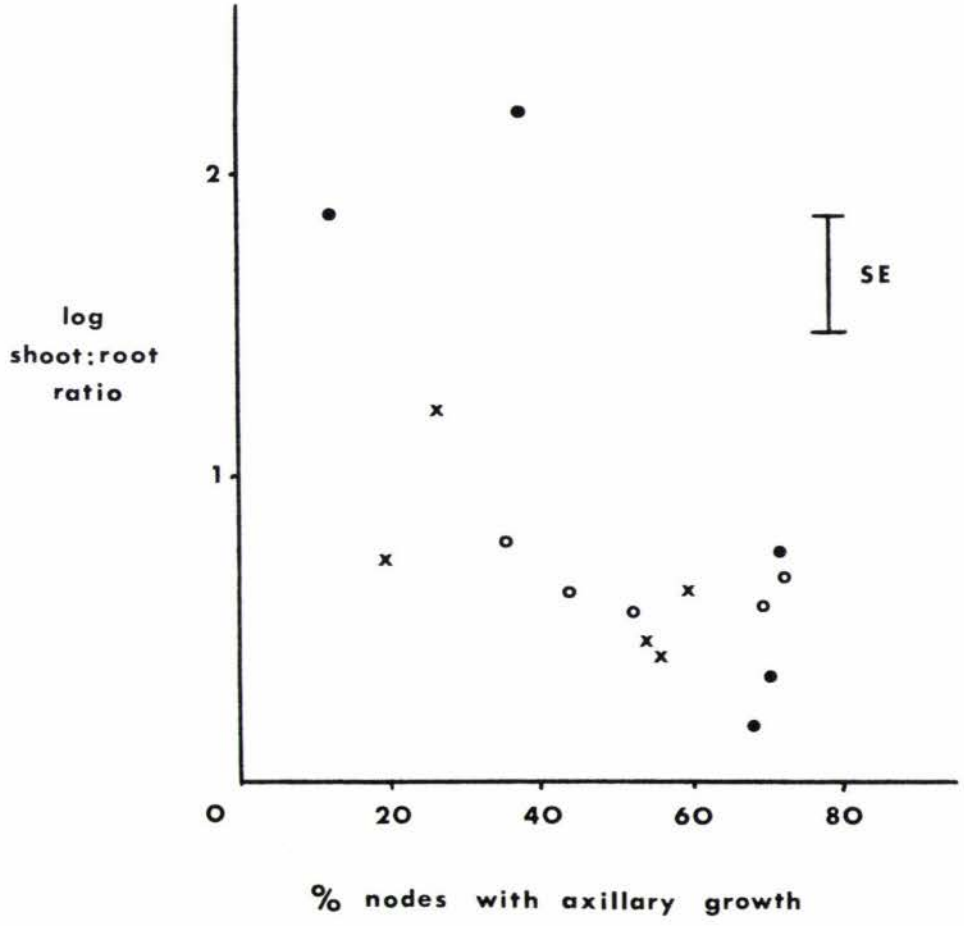
LSD 5% (body of table) = 0.59

TABLE III: The log shoot:root ratios of individual plants treated with 100 mg of glyphosate. See Appendix 3.15 for analysis of variance.

Replicate	Growth stage at treatment				
	Vegetat.	E. bud	L. bud	Flow.	Post-flow.
1	0.35	0.64	0.84	0.72	1.54
2	0.76	0.54	1.64	0.50	1.26
3	1.87	0.77	0.71	1.13	1.48
4	2.20	0.31	1.10	2.41	1.54
5	0.18	0.16	0.41	0.55	1.04
Mean	1.07	0.48	0.94	1.06	1.37

LSD 5% (means) = 0.97

FIGURE 7: The log shoot:root ratios of plants treated with 6.2, 25 or 100 mg glyphosate at different levels of maturity (as determined by percentage of nodes with axillary growth on the mother stem) during the vegetative growth stage. Coloured circles = 100 mg; crosses = 25 mg; empty circles = 6.2 mg.



was more noticeable at the higher rates of application. There was a highly significant correlation between log shoot:root ratio and percentage of nodes with axillary growth for the values shown in Fig 3 (ie 6.2, 25 and 100 mg treated plants) (Appendix 4). This effect seemed related more to stage of development than size of the treated stem as the correlation between log shoot:root ratio and height of treated stem was not significant for the same plants.

Although a large number of plants had necrotic stems when harvested, either due to senescence or the effects of glyphosate, most plants had at least some healthy sections of root remaining. There were small sections of necrosis and rotting in most root systems, including those of the untreated controls, and this was probably normal senescence. Root systems of treated plants often had less fibrous root material than control plants, this effect being more noticeable at higher treatment rates. In a number of these plants, small diameter connecting roots and rhizomes had also rotted away, leaving only lengths of root material 10-20 mm thick. These sections of root were healthy in appearance and viable (Plate 29).

(3) PLANT PARTS EXPERIMENT:

(a) Observations:

At 4 weeks after treatment, only five plants in this experiment showed the severe water stress condition leading to death discussed earlier, and these are indicated in Table IV. The plants which failed to regenerate after the main harvest also appear in this table.

In general, the closer to the base of the stem the glyphosate was applied, the greater the effect on untreated daughter stems. This was most noticeable for the "Lower Third" treatment. After 1 week, all daughter stems from this treatment were visibly affected whereas with other treatments, a few stems on each plant remained unaffected. Yellowing of the developing leaves in daughter stems was more severe with this treatment, and the yellowing was often accompanied by vertical necrotic lines and streaks on the main stems, and necrotic lesions on more mature leaves, especially on leaf margins. These latter symptoms were rarely seen on daughter stems in other treatments, except where glyphosate was applied to the lower half of the mother stem, as in the

PLATE 29: Roots of a Cirsium arvense plant at the second harvest. Fibrous root material is still present at the upper part of this root system. Root sections like those beside the ruler were the only remains of root systems in some plants.

TABLE IV: The eight most affected plants from the Plant Parts Experiment with their log shoot:root ratios. Plants seen wilting at 4 weeks after treatment, or which regrew after the main harvest, are indicated. See Appendix 2.6 for the log shoot:root ratios of the other plants treated in this experiment.

Treatment	Replicate	Log shoot:root ratio	Wilting	Regrowth
lower third	5	1.97	Yes	No
lower third	1	1.67	Yes	No
all parts	4	1.67	Yes	No
stem	3	1.62	Yes	No
mid third	5	1.30	Yes	No
side	1	1.22	No	Yes
lower third	3	1.15	No	No
all parts	5	1.04	No	Yes

"One Side" and "All Parts" treatments.

With almost all treatments, the flowers developing on the mother stem had white or brown florets 1 week after treatment. However, only about half of the flowers of each treated stem in the "Lower Third" treatment had discoloured florets after 1 week, although they were all dead by 4 weeks.

Untreated leaves on the upper parts of treated stems often developed necrotic lesions within a week of glyphosate application. Often the leaves on lateral shoots growing above the treated region also turned yellow, though those closer to the treated region tended to be affected more than those nearer the stem apex. When the leaves in the lower third of a stem were treated, the leaves on lateral shoots within the treated region often remained green while those further up the stem turned yellow. The lower lateral shoots generally made little growth during the stage of vegetative growth whereas the leaves which became yellow were those which were expanding at the time of treatment.

After 1 and 4 weeks glyphosate applied to the upper parts of stems had generally caused little effect on tissues below the treated area. Leaves developing on side shoots became yellow, distorted and necrotic, and occasionally orange-brown marks formed on the midribs of lower leaves near their point of attachment to the main stem. Otherwise, the lower parts of the plants usually remained unaffected, although general necrosis had often occurred by the main harvest, probably as a result of senescence.

All mother stems of the "Lower Third" treatment were totally necrotic at the main harvest. This was the only treatment in this experiment in which all treated stems died although complete necrosis did occur in four of the five treated stems from the "All Parts" treatment.

Glyphosate caused the least amount of damage to plants with treated buds or axillary leaves. After 4 weeks, the branch tips in the "Buds" treatment, and entire branches in the "Axillary Leaves" treatment, had become necrotic and withered. The rest of the mother stem was generally unaffected, although there was some degree of distortion of developing untreated side shoots lower down the stem. However, even with these treatments there was some translocation of glyphosate to daughter stems.

One week after treatment the younger daughter stems in two of the five plants in the "Buds" treatment, and in all five plants in the "Axillary Leaves" treatment, showed yellowing of young apical leaves and side shoots.

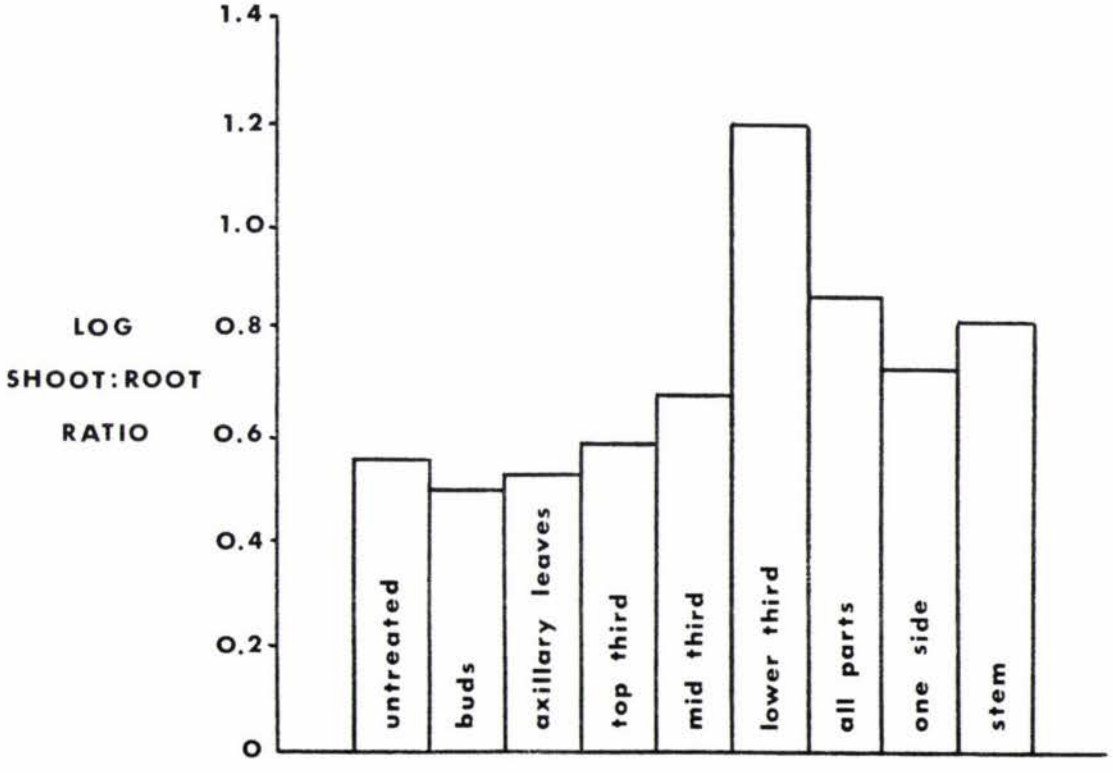
With the "Stem" treatment almost no yellowing of leaves developed on the treated stems though daughter stems showed the usual yellowing symptoms. The treated stem tissue became orange-brown in colour after 1 week and was necrotic after 4 weeks. Leaves on the treated stems developed necrotic lesions soon after treatment, especially around the margins and beside the major veins. All tissues on treated stems were necrotic above the lowest point of application after 4 weeks, but leaves and stem tissue at the bottom of the stem generally remained green.

One week after application in the "One Side" treatment, only a few flowers on branches directly opposite to the treated side had not turned brown or white. Axillary growth on the untreated side also tended to be less affected than on the treated side. However, these differences were not noticeable at 4 weeks, and the number of daughter stems affected by glyphosate was no different to that for plants with stems treated on both sides.

(b) Root Decomposition:

Fig 8 shows the results of glyphosate applied to different parts of the stem expressed in terms of the average log shoot:root ratio. An F-test showed the differences not to be significant at the 5% probability level (Appendix 3.10) though the differences between mean root dry weights were highly significant (Appendix 3.12). The response of the treated plants however was very variable. For example, the most effective treatment applied to the lower third of the stem resulted in the death of three plants (with log shoot:root ratios of 1.97, 1.67 and 1.15) while the other two were barely affected (values of 0.61 and 0.62). All plants which had log shoot:root ratios above 1.00 are listed in Table IV.

FIGURE 8: Average log shoot:root ratios of plants treated on different parts of the mother stem. LSD 5% = 0.65.



(4) LEAF SIDE EXPERIMENT:

The log shoot:root ratios of plants treated on the upper leaf surfaces were not significantly different from those of plants treated on the lower surfaces (Appendix 3.11). In fact, neither treatment resulted in log shoot:root ratios significantly greater than those of untreated plants (Fig 9).

However, although appreciable root decomposition did not occur, Fig 10 suggests that the shoot and root dry weights of treated plants were reduced. Root growth was very variable and the differences in root dry weight were not significant ($P<0.05$) (Appendix 3.13) though the reductions in shoot dry weight were highly significant ($P<0.01$) (Appendix 3.16). Treatments applied to the upper and lower leaf surfaces did not differ significantly in their effects on dry weight nor in the symptoms displayed.

(5) VARIABILITY WITHIN REPLICATES:

As has been found by other workers studying C. arvense (eg Verity 1981), considerable variability in herbicide susceptibility between replicates was observed in the present studies. Three factors, plant size, relative humidity, and plant sex, were investigated as possible sources of the variation.

Correlation coefficients between the log shoot:root ratio of all treated plants and various parameters of plant size and relative humidity were calculated and appear in Table V. No significant correlation was found between log shoot:root ratio and any of these parameters except for a slight correlation ($P<0.1$) with the average relative humidity for the 6 hr period following application.

In an attempt to determine whether male and female plants differ in susceptibility to glyphosate, the number of treated males with log shoot:root ratios exceeding their replicate mean was calculated. If male and female plants are equally susceptible, 50% of treated plants of each sex would be expected to be above the average value. Of the 59 treated plants positively identified as males, 49.2% had log shoot:root ratios above the average within their replicate.

FIGURE 9: Average log shoot:root ratios of plants treated on either the upper or lower leaf surfaces. LSD 5% = 0.45.

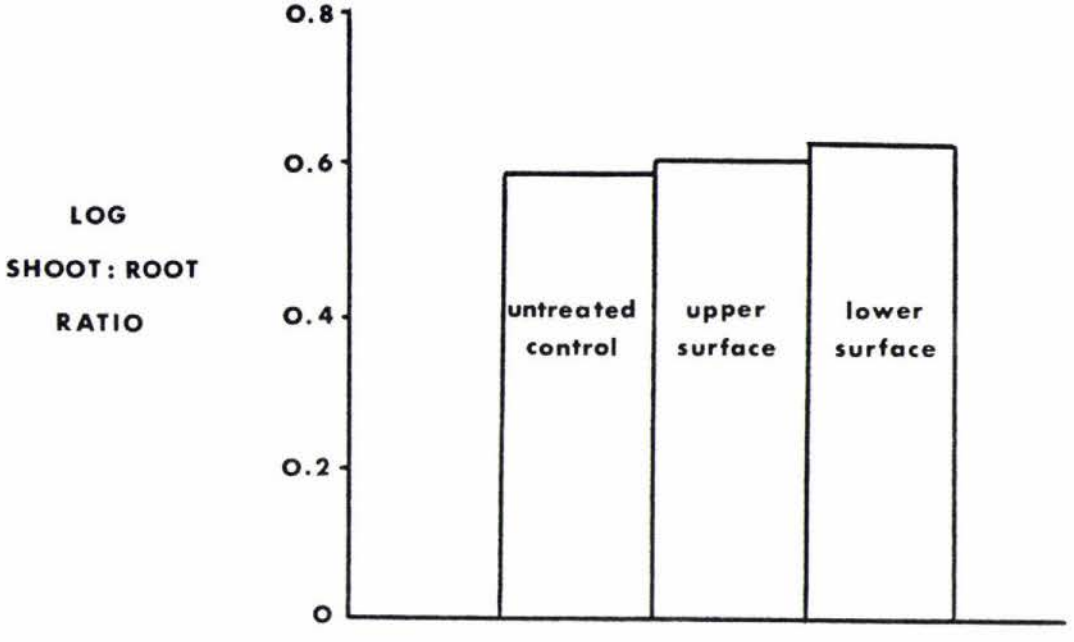


FIGURE 10: Average shoot and root dry weights of plants treated on either the upper or lower leaf surfaces.

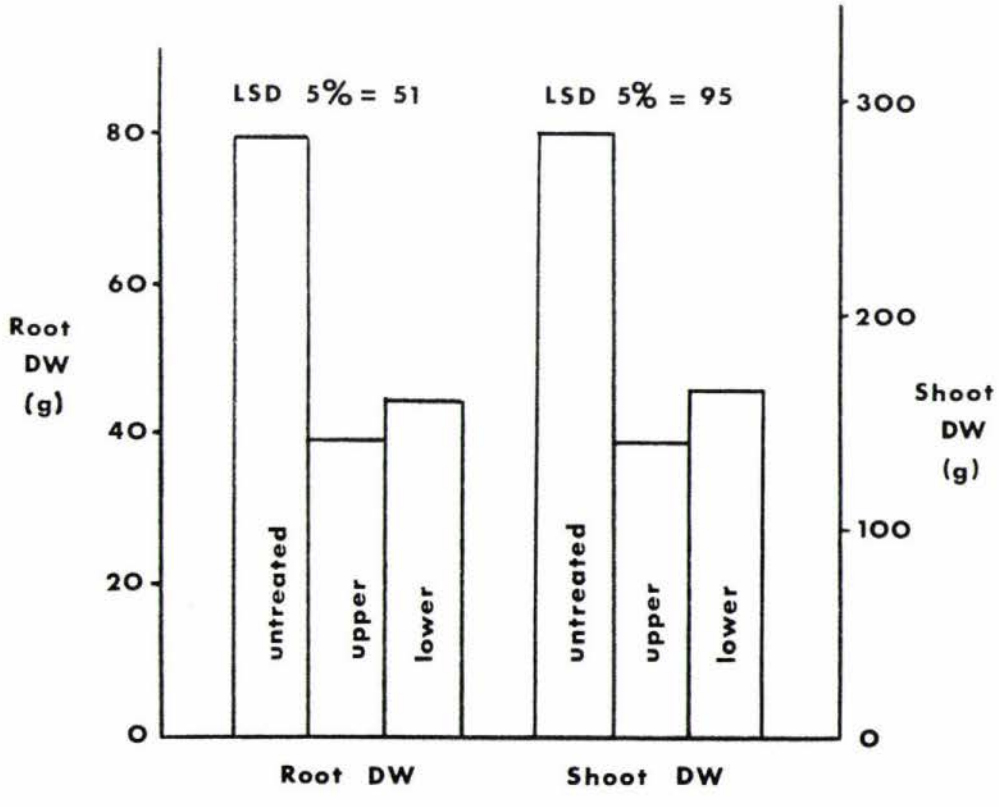


TABLE V: Correlation coefficients (r), using results from treated plants in all three experiments, between the log shoot:root ratio and the factors listed.

Factor	r
No. of stems per plant > 20 cm at treatment	-0.085 (NS)
Height of mother stem when treated	-0.007 (NS)
Relative humidity at time of treatment	-0.024 (NS)
Av. relative humidity for 6 hr following treatment	-0.151 (*)

NS = not significant at 10% level of probability

* = significant at 10% level of probability but not at 5% probability

As the sex of all plants was determined for this analysis, the data was also used to check the findings of Lloyd and Myall (1976) that the ratio of male:female C. arvense plants is 1:1. Of the 255 plants which were positively sexed (both experimental plants and spare plants not used in the trials), 45.1% were males. A chi-square analysis of this result showed it to be not significantly different from a 1:1 ratio of males:females (Appendix 5).

DISCUSSION

(1) GROWTH STAGE EXPERIMENT:

Table II shows that at least 100 mg of glyphosate was needed to obtain effective control of a C. arvense plant growing under the experimental conditions, with more being required at some growth stages. However, it must be emphasized that the chemical was applied to only one stem per plant in these experiments and there was an average of 7.5 stems per plant taller than 20 cm at the time of treatment (Table I). Further work is required to determine whether an application of glyphosate to one stem is as effective as the same amount applied in a number of smaller doses to all stems, the latter being more comparable with the field situation.

The present work was not aimed at determining the lethal dose of glyphosate on a per plant basis and only one stem per plant was treated so that translocation to daughter stems could be studied. The use of different application rates in the Growth Stage Experiment was partly to ensure that at least one dosage would cause sufficient effect to show up the differences in susceptibility between growth stages, and partly to study the differences between the lethal and sub-lethal effects.

Table III shows that, although plants were occasionally killed by 100 mg at most of the growth stages, consistent control was obtained only at the post-flowering stage. However the highly significant inverse correlation between maturity of plants treated at the vegetative growth stage (as measured by proportion of nodes with axillary development) and log shoot:root ratio (Fig 7) suggests that good control can also be obtained by application at the early vegetative stage.

A hypothesis that would explain these results is that glyphosate transported to the roots at growth stages not markedly affected by the herbicide was redirected to the developing daughter stems in the assimilate flow so that little herbicide remained in the roots. After flowering the end of the growing season was near and it is probable that few daughter stems were developing. Thus assimilates and glyphosate probably remained in the roots. Fig 6 provides evidence that a build up of root material occurred in the autumn. The average dry weight of the

roots of untreated plants in late March was 39.1 g, whereas in late June it was 136.7 g (Appendix 2). Plants treated in February (post-flowering) were therefore more likely to send assimilates to the roots for storage than plants treated in December.

The experimental plants may not have been typical of plants in the field during the early vegetative stage. In the field C. arvense plants are thought to develop mainly vegetatively from root sections (Amor and Harris 1975), whereas the experimental plants were grown from seed. The former type of plant draws on reserves from the parent root section while establishing (Hodgson 1968), whereas no upward translocation of assimilates from the root would be possible in the latter.

It seems probable that in plants treated at the early vegetative stage translocation of assimilates would have been in a downwards direction to support root growth. In plants treated after the mother stem had developed axillary growth in more than 50% of the nodes, root development may have been complete and assimilates together with glyphosate could have been moving into the developing daughter stems.

Thus it would seem unwise to extrapolate the results from the early vegetative plants in the present trial to the field situation if most C. arvense development there is by vegetative reproduction. From the practical point of view it is doubtful if plants could be treated with a ropewick applicator at the early vegetative stage as they would be too short. Although Table I shows that all plants treated at this stage were more than 30 cm high, stems in the field are usually less than 20 cm at the stage when 50% of the nodes have developed axillary growth. Obviously stem height would not be a consideration in situations where a selective treatment was not necessary as the whole plant could be sprayed.

(2) ROOT DECOMPOSITION:

There appear to be two possible reasons for the disappearance of fibrous roots and smaller connecting roots and rhizomes in plants affected by glyphosate. Sagar and Rawson (1964) claim that only large root sections are left to overwinter in the normal field situation. The observation in the present work that fibrous roots and small rhizomes in some

untreated plants harvested late in autumn were showing signs of decomposition supports this statement. Treated plants with roots showing the same effects may have been undergoing early senescence.

The other possibility is that the root tissues which rotted away contained glyphosate, whereas the unaffected roots did not. Devine (1981) found that 14-C-labelled glyphosate accumulated in the fibrous roots of C. arvense. In Cyperus rotundus Zandstra and Nishimoto (1977) found that it travelled with assimilates through tubers full of food reserves, without affecting them, and accumulated in the partially filled tubers. The healthy sections of C. arvense root observed here may likewise have been already filled with food reserves or, alternatively, have been accumulating assimilates from untreated stems, or not accumulating assimilates at all. Under such conditions glyphosate would have passed through these sections of root without affecting them. This second hypothesis could explain why some sections of root of a certain size survived while others of similar size were killed.

Whatever the reason, it was very seldom that treated plants did not have at least one healthy section of root when harvested. This ability of the plant to keep part of its root system unaffected by the herbicide is no doubt one reason for the difficulty in obtaining complete control of C. arvense. It is possible though that if all stems had been treated instead of just one per plant fewer sections of root would have escaped damage.

(3) PLANT DEATH:

Although glyphosate affected chlorophyll synthesis, dormancy mechanisms and growth rates, and caused distortion and necrosis of foliage, death of the plant appeared to be caused by a different mechanism. The few plants in which the entire shoot system did die apparently had their water supply disrupted, resulting in death by desiccation. Because all stems were affected simultaneously this was probably the result of an effect on the root system rather than the vascular system of each stem.

The ability of glyphosate to kill plant cells was always shown on treated plants by its ability to cause leaf necrosis. It is possible that necrosis also occurred in the roots and, if enough of the root system was damaged, could have resulted in the cessation of water uptake and thus led to dehydration of the stems. Verity (1981) found no evidence of necrosis in C. arvense roots 8 days after treatment with 12 mg ai glyphosate. However, Saidak and Marriage (1976) did observe glyphosate-induced necrosis of the roots 14 days after treatment with doses as low as 10 mg/plant, and 40 mg/plant killed more than 90% of the root system after 24 days.

The delay of several weeks before the wilting of stems occurred could thus be explained by the time required for root necrosis to develop. In the many cases where wilting did not occur, necrosis of the roots was presumably not extensive enough to affect water supply to the stems.

(4) REGROWTH:

Low rates of glyphosate tended to increase the number of regrowth stems appearing above the soil surface (Fig 4), though the increase was not statistically significant. Further evidence of a genuine effect was found when the roots were examined and large numbers of young shoots were observed, many of which had failed to reach the soil surface. Glyphosate was apparently stimulating this development (ie acting as a hormone) or affecting the mechanism which would normally prevent such development (ie interfering with a hormone).

The reduced regrowth noted late in autumn could be interpreted as an adaptation to prevent wasteful use of root reserves in producing stems which would be unlikely to survive the winter. Henson (1969) measured similar reductions in regrowth of C. arvense root sections at the onset of short days, reduced temperature and senescence cf top-growth. The fact that regrowth was occurring at all in the present trials was probably a result of favourable growing conditions in the glasshouse.

(5) SYMPTOMS:

Glyphosate-induced chlorosis was probably caused by inhibition of chlorophyll formation rather than destruction of existing chlorophyll. Without exception, tissues affected by chlorosis were at a very early stage of development at the time of treatment. The appearance of the plants suggested that when glyphosate entered the developing leaves, the parts which had already formed chlorophyll remained green while the rest of the leaf continued expanding but did not develop chlorophyll. This suggests that the first leaf cells to form chlorophyll are those at the tips of lobes and beside vascular tissue as these were the parts of partially chlorotic leaves which were green. The fact that larger leaves never became chlorotic, even when directly treated with glyphosate, is another indication that chlorophyll degradation did not occur.

Williams (1956) states that it is common in cases of mineral deficiency or virus attack for loss of chlorophyll to be confined either to narrow fringes along the main veins, or to all parts of the lamina except these fringes (as occurred in the present trial). The main expanses of the mesophyll behave as tissues physiologically distinct from the main veins and their immediate environs. Furthermore, he states that the main veins of leaves react to auxins as if they were stems, whereas the main expanses of mesophyll are indifferent to auxin.

This latter phenomenon could be of relevance to the distortion caused by glyphosate in young C. arvense leaves. Growth appeared to continue along the longitudinal axis within such leaves while lateral expansion of the leaf surface was severely reduced.

Most C. arvense axillary buds develop into shoots during the vegetative stage. However only one or two leaves are produced in lower axils while axillary buds in the top third of a stem develop into flowering branches. Between these two zones short branches develop which may elongate further and develop flowers once the upper branches have finished flowering. This differential development of axillary growth is probably under hormonal control and so the production of abnormally long axillary branches from lower nodes which was observed following glyphosate applications may be caused by disruption of this hormonal control by the herbicide. As with the effect on regrowth, an

alternative possibility is that glyphosate was stimulating elongation of these branches.

Another glyphosate-induced phenomenon which may be connected with a disruption of hormonal control within the plant was the apparent change in sex noticed with some flowers. Glyphosate could apparently cause male flowers to become females, whereas the reverse situation was never observed. Galoch (1978), studying sex expression in another dioecious plant, Cannabis sativa, found that auxin, ethylene and kinetin have a feminizing effect while gibberellins promote masculinization.

IAA (indole-3-acetic acid) (auxin), a plant hormone produced by apical meristems, is known to inhibit axillary growth (Devlin 1975) and it is possible that the increased growth of side branches caused by glyphosate in the present work could be due to inhibition of IAA synthesis. An alteration of IAA concentrations may also explain the observed sex change of flowers and the distortion of leaves. Tryptophan is the precursor of IAA (Devlin 1975) and, as can be seen in Fig 2, the latest suggestions to explain the mode of action of glyphosate postulate interference with the enzyme 5-enolpyruvyl-shikimate-3-phosphate synthase which would result in inhibition of tryptophan production (Hollander and Amrhein 1980). None of the earlier schemes proposed to explain the mode of action of glyphosate suggested any effect on the production of this amino acid. However, Lee (1982) obtained results from tobacco callus experiments which suggest that glyphosate depletes the level of free IAA through rapid acceleration both of conjugate formation and of oxidative degradation of IAA, not by inhibition of production.

(6) TRANSLOCATION:

(a) Symplastic:

Some of the evidence suggested that glyphosate moved "from source to sink" in the plants. One example was the chlorosis of young developing tissue both on the treated mother stem and associated untreated daughter stems, followed by distortion and necrosis in these regions, while more mature regions remained unaffected. The specificity of the tissues affected was often still evident at the main harvest when the tops of affected stems were very small, distorted and sometimes necrotic, while

leaves and stem tissue immediately below were normal in size, shape and colour, showing that growth had continued completely free of the effects of glyphosate.

Such effects do not provide absolute proof of symplastic movement as the apical tissues may have been the only parts affected not because glyphosate did not reach other parts but because no other parts were at a susceptible stage of development. However, in studies with radiolabelled glyphosate several workers including Sprankle et al (1975b) and Devine (1981) have found accumulation in areas of high meristematic activity which supports the "source to sink" proposal.

For glyphosate to have reached untreated daughter stems symplastic movement from the treated stem must have occurred as movement in the apoplast would have been acropetal, not basipetal against the transpiration stream.

(b) Apoplastic:

Dewey (1981) found that glyphosate was transported via the transpiration stream to all transpiring tissues above the site of application in the herbaceous dicotyledon Ipomoea purpurea. In most cases all tissues on treated C. arvense stems above the lowest point of glyphosate application eventually became necrotic in the present experiments, suggesting that apoplastic movement of the herbicide was occurring in the manner observed by Dewey. This proposal is supported by the fact that many of the affected leaves were fully mature, making it seem unlikely that transport in the phloem was involved.

Although tissues above the points of glyphosate application became necrotic, tissues lower down the stem (ie "upstream" of the apoplastic water flow) were not affected. As a result, treated stems were totally killed only if the application was made to the lower parts of the stem, unless the wilting form of death occurred in which case the whole plant died.

Verity (1981) found that 14-C-glyphosate accumulated at the margins of mature C. arvense leaves and used this observation as evidence of apoplastic movement. Necrosis on mature leaves in the present experiment was often noted as initially developing at the leaf margin.

However, necrosis of mature leaves was also observed occasionally on badly affected daughter stems. The probable explanation of this effect is that glyphosate was moved to the daughter stems in the phloem, and when a sufficient concentration was present, it leaked from the phloem into the xylem, either in the roots or the daughter stems. It is suggested that glyphosate moves only in the phloem at low concentrations (as in lightly affected daughter stems) and in both phloem and xylem at high concentrations (as in treated stems and badly affected daughter stems).

(7) TRANSLOCATION TO DAUGHTER STEMS:

Assuming that glyphosate does move to daughter stems in the assimilate flow, it is interesting to note the extent to which assimilates were translocated from mother to daughter stems. One disadvantage of using symptom expression rather than labelled material to follow translocation is that the proportions of glyphosate that remained in the roots or accumulated in daughter stems are unknown. Observations of root damage and symptom intensity in daughter stems, however, do suggest that more glyphosate remained in the roots and less moved into daughter stems at the post-flowering than at earlier growth stages, supporting the hypothesis discussed earlier regarding the increased susceptibility of plants following flowering.

Using symptom expression it was not possible to gauge accurately the relative amounts of glyphosate translocated into mature daughter stems compared with young stems because of the different types of symptoms involved. However, it did seem that more was moved into young daughter stems than older ones. This conclusion was reached by comparing the damage to stems of different ages when treated with the same amount of glyphosate and using this knowledge of differential stem susceptibility to decide if one daughter stem received more herbicide than another. Greater translocation into young stems is what would be expected if movement was occurring from source to sink. Mature stems would not be requiring assimilates whereas young stems would be expected to need additional assimilates to assist growth in the shade of the older stems, and also to help them reach maturity before the onset of winter as determined by day length.

One point made clear by a study of symptom expression was that glyphosate movement to daughter stems was influenced by more than just stem maturity. On a single plant daughter stems apparently identical in size and maturity were often affected very differently. The differences in degree of effect may well have been due to varying distances of the daughter stems from the treated stem but no evidence is available on this point.

(8) PLANT PARTS EXPERIMENT:

Of the plants similar in maturity in the Growth Stage Experiment to those treated in the Plant Parts Experiment, none treated with 25 mg of glyphosate, and few of those treated with 100 mg, had log shoot:root ratios above 1.00 at the time of harvest, indicating only minor effects on the root system. As shown in Table IV, however, eight of the plants treated with 25 mg in the Plant Parts Experiment exceeded this value, showing a much greater effect. With all of these plants glyphosate was applied to the lower parts of the mother stem, whereas application was to the upper parts of stems, as would occur with ropewick application, in the Growth Stage Experiment. Only with the 100 mg treatments did any glyphosate get applied to leaves in the lower half.

The root decomposition data and observation of symptoms both suggested that more glyphosate was translocated to the roots and daughter stems when it was applied to lower rather than upper parts of the stem. Several reasons for this appear possible. Firstly, more of the chemical may have been absorbed in the lower parts of the stem. McWhorter et al (1980) and Wills (1980) have shown that more glyphosate is absorbed by older than younger leaves in soybeans and cotton respectively. The older leaves in the present trial were more likely than younger leaves to have broken leaf surfaces due to the effects of insects and the spines of other leaves. It is also possible that conditions were more favourable for absorption lower down the stems. There was a very noticeable vertical gradient in temperature within the glasshouse, the air being cooler near the base of the plants because of shading and the movement of water through the felt mats from the soak hoses, while air temperatures above the plants often reached 30 C during the hottest part of the day. The humidity would also have been higher near the wet mats and the lower temperature combined with higher humidity would be

expected to have reduced the drying rate of glyphosate solution applied to the lower leaves, thus allowing more time for absorption.

Secondly, the lower were more likely than the upper leaves to have translocated glyphosate to the roots. Biddulph and Cory (1965) have shown that, in bean plants, assimilates are mostly translocated to the roots from leaves near the base while translocation from the upper leaves is mainly towards the stem apex and developing leaves. In the experimental plants the lower leaves had stopped growing so that the majority of assimilates would have been exported. The upper leaves, however, were mostly still expanding and so would be expected to have exported a smaller proportion of the assimilates. With application to the upper leaves, therefore, less translocation of glyphosate out of the treated zone would be expected. Senescence always began in the leaves near the base of the stems, and as the lower leaves treated in the Plant Parts Experiment were showing the first signs of senescence at treatment, breakdown and export of structural materials from these leaves was probably occurring.

If the entire length of stems had been treated in the Growth Stage Experiment, it is possible that more effective control of plants at the bud and flowering stages would have been obtained. It was at these stages that Marriage (1980) considered glyphosate to give the best results. However, the aim of the present studies was to obtain information on the action of glyphosate applied by the ropewick application technique so that applications were made to the upper parts of the stem. It is unfortunate that it was necessary to apply glyphosate to the lower part of the stem for the 100 mg treatments as it is uncertain whether 100 mg was significantly more effective than the 25 mg treatment because of the higher dosage or simply because leaves lower down the stem were treated.

Verity (1981) considered that much of the glyphosate applied to *C. arvense* plants by ropewick applicators is deposited on the stem. Results from the present trial support those of Wills (1978) and McWhorter *et al* (1980) in that the stem seemed to be just as efficient as, if not more efficient than, the leaves in absorbing glyphosate.

If a ropewick applicator made only one pass over a C. arvense plant, one would expect chemical to be applied to one side of the stems only. The present recommendation is that a double pass should be made to increase the amount of glyphosate applied to plants (Monsanto 1982), and this helps to ensure treatment on both sides. Results from this experiment suggest that the distribution of glyphosate through the plant with one-sided application is no less effective than with application to two sides.

(9) LEAF SIDE EXPERIMENT:

Verity (1981) claimed that glyphosate applied to C. arvense leaves with a ropewick applicator would tend to be deposited mainly on the lower surfaces. The data in Fig 10 and the observations made of plants in this experiment suggest that there is little, if any, difference in absorption between the two surfaces, so that one side has no great advantage over the other. There may have been small differences which could not be detected with the experimental technique used but, as mentioned above, ropewick applicators apply much of the glyphosate to the stem, which appears to be as efficient at absorption as leaves, thus probably making small differences in leaf absorption unimportant.

(10) VARIABILITY WITHIN REPLICATES:

Plant size at treatment was suggested as a cause of variability in results because a small plant would receive a greater amount of glyphosate per gram of tissue than a large plant treated with the same dose. It was not possible to obtain a precise measure of total plant size, including roots, at treatment. Measurements were made of the height of the treated stem and of the number of stems over 20 cm but neither measure was very satisfactory and the lack of correlation between these two parameters and the log shoot:root ratio does not entirely discount the possibility that some of the variability in results was due to variations in plant size.

Relative humidity was investigated because Gottrup et al (1976) found that C. arvense absorbed three times as much glyphosate under high as under low humidity conditions. The average relative humidity during the

6 hr after treatment was calculated using data from hygrothermographs in the glasshouse, this period being taken because glyphosate deposits on the leaves had usually dried after 6 hr.

Relative humidity fluctuated greatly within the glasshouse. During the day when the sun was shining into the glasshouse and the ventilators were all working, it often fell below 40%. At night the ventilators were closed, causing a build up of moisture helped by the presence of the wet felt mats and resulting in levels above 95%. Due to the time needed to treat individual plants it was not possible to apply all treatments at the same time of the day. Some plants were treated as early as 10 am while others were treated as the sun was setting. Thus the humidity for the 6 hr period following application varied greatly, in spite of which there was only a very small correlation between relative humidity and glyphosate activity.

Rolston (1974) found that absorption of picloram by Ulex europaeus was significantly increased if herbicide deposits on the plants were re-wetted with a mist of water after they had dried, allowing further absorption to occur. The interior glasshouse walls in the present trial were always covered in condensation during the night, and it seems possible that glyphosate deposits on the leaves may have been re-wetted at this time by condensation dripping from the roof. Any re-wetting of this type would be expected to mask any differences in absorption due to differences in humidity immediately after application.

Although the trial was not designed to test differences in susceptibility between male and female plants, the results obtained gave no indication of any such differences existing. However, as with the other parameters investigated as possible sources of variation, an experiment designed specifically to investigate whether susceptibility to glyphosate is affected by plant sex would need to be conducted to confirm this finding.

The plants used in this work were grown from seed and therefore probably included several different ecotypes. By using plants grown from root cuttings of a single clone it may have been possible to obtain greater uniformity. However, it was not practicable to establish the large number of plants required from root cuttings, and Verity (1981) noted large variations in growth between plants even with plants raised by

this propagation method.

Nevertheless, it is probable that some of the variation observed in the present work was due to ecotypic differences in glyphosate susceptibility such as have been shown to exist in C. arvense by Saidak and Marriage (1976). There was considerable variation in the appearance of the plants grown. Plates 30 and 31 show untreated plants together in the glasshouse in the same microclimate, one of which has leaves which are much flatter and less prickly than the other. Both types were common in the experimental plant population. In a third type which was less common the phyllaries had bright purple tips, while another, also uncommon, had white flowers in contrast to the usual mauve colour. As the plants were all grown under very similar conditions, it is probable that the differences in morphology were due to genetic rather than environmental influences. However, the effects just described were clearly defined only in some plants while most displayed one or more of these traits to lesser degrees. As a result, it was not possible to place plants into groups based on morphological differences.

(11) PRACTICAL IMPLICATIONS:

The present recommendation for glyphosate application to C. arvense is that treatments should be applied between flower bud development and before autumn brown-off (Monsanto 1982). Results from the present studies suggest that more reliable control is likely to result from treatment in the later stages of this suggested period. Moore (pers. comm.) states that ropewick application late in the season tends to strain the equipment as the plants become "very woody" at this time. However, it should be possible to strengthen and modify existing equipment to cope with this extra strain if better control levels are likely to be obtained.

The other major practical consideration to arise from this work is the importance of applying the glyphosate as low as possible down the stems. The use of booms supported above the ground by skids on either end could possibly allow lower application to be made safely. Once again the booms might need to be strengthened to withstand the extra stress of pushing through stands of thistles at relatively low heights.

PLATE 30: A vegetative stem of an untreated plant with flat leaves.

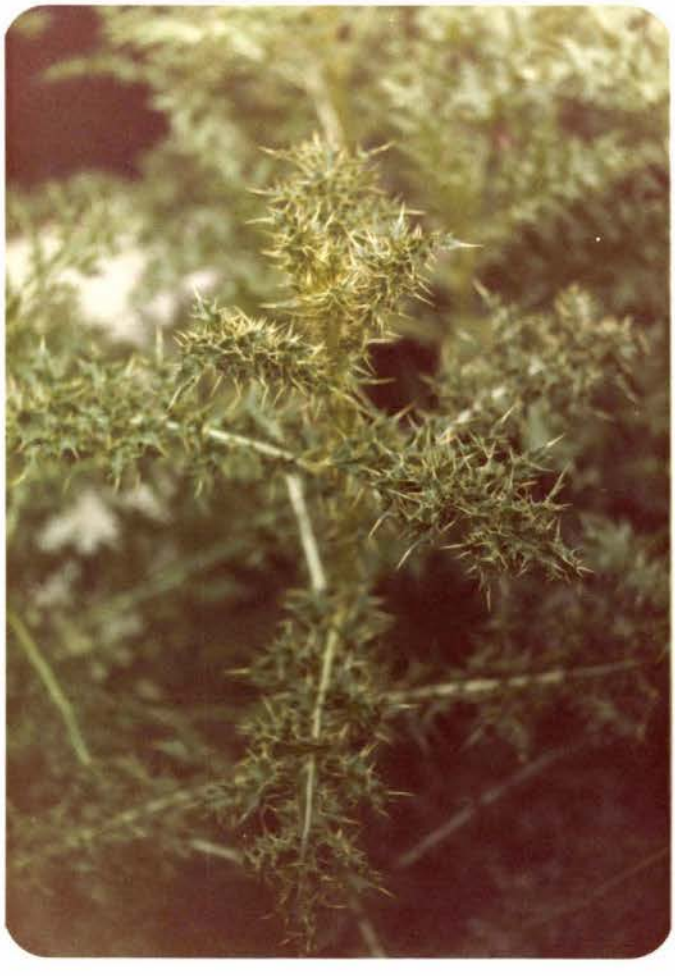


PLATE 31: A stem similar in all respects to that in Plate 30 except in its leaf morphology and thus presumably also in its genotype.

Observations of the initially weak regrowth from partially affected plants indicates that competition from vigorous pasture growth encouraged by appropriate management at the time regrowth of thistles is occurring could help to prevent establishment of regrowth. The recovery of some daughter stems observed in the experiments despite distortion at the apex and a temporary reduction in vigour suggests that in the absence of competition a greater degree of recovery from the effects of glyphosate is likely to occur.

If the symptoms noted in these trials also occur in the field, then the appearance of wilting 4 weeks after treatment, which indicated complete death of the roots, may be a useful field indication of the effectiveness of control as present evaluation techniques require waiting until regrowth occurs in the following spring.

As with most glasshouse studies the findings of the present experiments need to be confirmed in the field before any firm recommendations can be made. Conditions in the glasshouse were very artificial. Growth conditions tended to be ideal with plentiful supplies of water and nutrients and protection from extremes of temperature. As a result, plants tended to make faster and softer growth than is usual in the field. They were protected from most disease and pest problems and were grown in very small volumes of soil so that horizontal root development was very restricted. As a result, daughter stems developed very close to one another leading to shading problems. Also there was very little air movement in the glasshouse, causing the plants to become brittle with none of the flexibility found in plants which develop in the wind. It is not clear how such morphological differences would affect the uptake, movement and activity of glyphosate, but it is very likely that there would be differences, the importance of which could only be assessed by a comparable series of field experiments.

Another major point which needs further research is the importance of C. arvense seed in producing new plants. Seeds are generally thought to be unimportant in producing new plants due to the slow development of seedlings (Amor and Harris 1975). However, this should be investigated further before recommendations are made to apply glyphosate at the post-flowering stage which would permit production of viable seeds.

CONCLUSION

Glyphosate was translocated extensively throughout Cirsium arvense plants in the phloem to actively growing tissue, both within the treated stem and to untreated daughter stems. It destroyed roots most effectively when applied to post-flowering stems, probably due to assimilates accumulating in root tissue for storage at this growth stage rather than being translocated to developing daughter stems.

More glyphosate accumulated in roots and untreated daughter stems when it was applied to tissue on the lower parts of stems. Greater absorption and a greater degree of basipetal translocation were probably both responsible for this effect.

When present in large quantities, glyphosate also travelled in the apoplast, probably due to leakage from phloem to xylem once concentrations exceeded a certain threshold value. This resulted in accumulation of the chemical in all transpiring leaves above the treated part of the stem. Thus it appears that glyphosate will move into all parts of a stem only if applied near the base because movement into mature tissues can occur only in the apoplast.

Glyphosate acted in a number of ways. It caused chlorosis and affected hormonal control of growth, probably through inhibition of chlorophyll production and reduction of auxin levels respectively. It reduced or inhibited growth of stems and roots, with foliar distortion sometimes occurring due to some types of cells being more susceptible than others. Some tissues were actually destroyed, causing necrosis, and it was probably destruction of root tissues leading to dehydration which resulted in entire plant death on the few occasions that this occurred.

There appeared to be no major differences between stem and leaf tissue, or between upper and lower leaf surfaces, in the absorption of glyphosate.

C. arvense displayed much variability both in its growth and its susceptibility to glyphosate. Further research is required to determine the major factors responsible for differences in susceptibility.

On the basis of these findings, field trials should be conducted to confirm whether increased control of this weed can be achieved by treating at the post-flowering growth stage and by applying the chemical as close as possible to the ground without contacting pasture plants. The importance of seed in producing new plants also needs to be clarified before post-flowering application can be advocated.

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APPENDIX 1

Characteristics of plants at the time of treatment. Dose = dosage in mg ai glyphosate/plant; Trmt = treatment; Rep = replicate; Hgt = height of mother stem (cm); Node = number of nodes on mother stem; % ax = percentage of nodes with axillary bud development; Buds = number of flower buds present on mother stem; Flow = number of flowers present on mother stem; D>20 = number of daughter stems exceeding 20 cm in height; Sex = sex of the plant. Note that some plants could not be sexed due to dying before flowering or because all flowers produced were too distorted to be identified. Also included with these tables is the mean relative humidity data for the 6 hr period following treatment (RH) and the log shoot:root ratios (lSRR) of plants when harvested. This final parameter has been included so that variability in these values can be compared with variability in the other parameters.

1.1 Growth Stage Experiment - Vegetative Treatment

Dose	Rep	Hgt	Node	% ax	D>20	Sex	RH	1SRR
0	1	47	29	0	8	M		1.36
0	2	51	25	56	4	F?		0.64
0	3	71	31	77	5	M		1.11
0	4	42	25	24	3	F		0.43
0	5	46	29	34	3	M		0.77
0	Mean	51	28	39	4.6			0.86
1.5	1	46	27	33	4	M	63	0.68
1.5	2	65	25	64	7	M	85	0.57
1.5	3	38	23	52	4	M	80	0.29
1.5	4	62	28	32	4	F	87	0.74
1.5	5	39	23	74	1	F	93	0.60
1.5	Mean	50	25	51	4.0		82	0.58
6.2	1	35	23	43	1	F	60	0.62
6.2	2	65	25	72	11	M	85	0.67
6.2	3	55	20	35	4	F	80	0.78
6.2	4	48	26	69	3	F	87	0.57
6.2	5	42	29	52	3	F	93	0.55
6.2	Mean	49	25	56	4.4		81	0.64
25	1	47	27	56	5	?	56	0.40
25	2	53	27	59	5	?	88	0.63
25	3	53	23	26	11	?	68	1.22
25	4	30	26	19	1	?	83	0.72
25	5	52	24	54	0	?	87	0.46
25	Mean	47	25	44	4.4		76	0.68
100	1	46	27	70	13	?	55	0.35
100	2	69	28	72	8	?	78	0.76
100	3	63	26	12	6	?	64	1.87
100	4	46	30	37	2	?	78	2.20
100	5	52	28	68	4	?	85	0.18
100	Mean	55	28	50	6.6		72	1.07
	MEAN	50.5	26.2	47.6	4.8		78	0.77

1.2 Growth Stage Experiment - Early Bud Treatment

Dose	Rep	Hgt	Node	% ax	Buds	D>20	Sex	RH	1SRR
0	1	95	37	84	21	7	F		0.80
0	2	99	35	89	26	4	F		0.88
0	3	111	49	80	30	6	M		0.87
0	4	104	40	82	25	3	F		0.71
0	5	118	41	80	14	6	F		0.90
0	Mean	105	40	83	23	5.2			0.83
1.5	1	98	39	77	20	3	M	100	0.67
1.5	2	84	33	73	34	5	F	100	0.86
1.5	3	97	35	77	22	2	M	62	0.67
1.5	4	116	45	82	25	4	M	68	0.71
1.5	5	95	38	89	24	2	F	59	0.59
1.5	Mean	98	38	80	25	3.2		78	0.70
6.2	1	95	37	89	18	6	F	98	0.37
6.2	2	73	44	75	25	3	M	100	0.87
6.2	3	98	33	91	46	8	M	62	0.71
6.2	4	88	38	84	30	1	F	66	0.92
6.2	5	109	39	92	23	5	M	59	0.51
6.2	Mean	93	38	86	28	4.6		77	0.68
25	1	90	42	88	17	7	F	95	0.42
25	2	91	42	76	26	3	?	100	0.76
25	3	97	38	84	24	3	F	65	0.45
25	4	120	42	93	22	6	M	58	1.02
25	5	90	43	77	10	4	F	57	0.83
25	Mean	98	41	84	20	4.6		75	0.70
100	1	94	35	80	19	5	F	94	0.64
100	2	105	44	89	54	9	F	100	0.54
100	3	102	39	90	39	11	M	66	0.77
100	4	118	36	36	26	6	M	58	0.31
100	5	97	48	98	16	7	M	57	0.16
100	Mean	103	40	80	31	7.6		75	0.48
	MEAN	99.4	39.7	82.4	25.4	5.1		76	0.68

1.3 Growth Stage Experiment - Late Bud Treatment

Dose	Rep	Hgt	Node	% ax	Buds	D>20	Sex	RH	1SRR
0	1	155	46	96	67	7	F		0.28
0	2	154	46	100	79	6	M		0.44
0	3	160	43	100	61	4	F		0.20
0	4	180	39	100	94	6	F		0.68
0	5	135	43	79	29	8	M		0.62
0	Mean	157	43	95	66	6.2			0.44
1.5	1	138	37	95	58	8	F	96	1.05
1.5	2	151	51	100	85	9	F	97	0.34
1.5	3	128	46	100	35	3	M	90	0.42
1.5	4	153	55	100	65	5	M	100	0.59
1.5	5	162	54	100	68	7	F	88	0.62
1.5	Mean	146	49	99	62	6.4		94	0.60
6.2	1	153	44	100	52	4	F	95	0.40
6.2	2	173	42	95	103	2	F	96	0.27
6.2	3	120	38	100	45	5	?	89	0.67
6.2	4	181	49	100	115	12	M	100	0.44
6.2	5	144	43	84	44	10	M?	86	1.45
6.2	Mean	154	43	96	72	6.6		93	0.65
25	1	139	42	95	69	5	M	94	0.54
25	2	96	49	49	13	10	M	93	0.32
25	3	156	46	63	57	3	M?	88	0.23
25	4	177	49	94	117	10	F	100	0.49
25	5	156	52	90	42	15	M	84	0.20
25	Mean	145	48	78	60	8.6		92	0.36
100	1	116	41	63	63	5	?	93	0.84
100	2	143	42	86	75	4	M	84	1.64
100	3	137	45	91	56	3	?	80	0.71
100	4	150	46	100	153	6	F?	100	1.10
100	5	168	53	98	76	6	F	78	0.41
100	Mean	143	45	88	85	4.8		87	0.94
	MEAN	149.0	45.6	91.5	68.8	6.5		92	0.60

1.4 Growth Stage Experiment - Flowering Treatment

Dose	Rep	Hgt	Node	Buds	Flow	D>20	Sex	RH	lSRR
0	1	167	40	70	24	14	F		0.39
0	2	101	35	16	14	6	M		0.36
0	3	147	40	24	45	6	F		0.17
0	4	132	32	75	15	6	M		0.55
0	5	128	35	71	36	7	F		0.10
0	Mean	135	36	51	27	7.8			0.31
1.5	1	143	32	23	31	8	F	79	0.10
1.5	2	144	41	78	31	6	M	70	0.46
1.5	3	129	37	23	23	11	F	90	0.37
1.5	4	155	42	116	34	5	M	67	0.67
1.5	5	159	45	83	32	8	F	72	0.48
1.5	Mean	146	39	65	30	7.6		76	0.42
6.2	1	132	42	28	22	6	F	77	0.07
6.2	2	116	27	17	14	12	M	68	0.49
6.2	3	158	44	66	29	7	F	85	0.45
6.2	4	130	45	13	14	7	M	67	0.79
6.2	5	104	64	54	12	12	F	68	0.41
6.2	Mean	128	41	38	27	8.8		73	0.44
25	1	142	35	39	33	3	F	63	0.26
25	2	144	46	115	24	9	M	66	0.42
25	3	122	43	41	27	10	F	76	0.60
25	4	153	42	50	17	6	M	68	0.29
25	5	129	43	19	12	11	F	60	0.98
25	Mean	138	42	53	23	7.8		67	0.51
100	1	166	44	68	40	6	F	54	0.72
100	2	145	44	56	17	6	M	62	0.50
100	3	174	43	74	59	4	F	70	1.13
100	4	168	49	51	43	8	M	69	2.41
100	5	154	43	56	41	10	F	53	0.55
100	Mean	161	45	61	40	6.8		62	1.06
	MEAN	141.7	40.6	53.4	29.2	7.8		69	0.55

1.5 Growth Stage Experiment - Post-flowering Treatment

Dose	Rep	Hgt	Node	Buds	Flow	D>20	Sex	RH	lSRR
0	1	156	39	3	63	4	F		0.61
0	2	163	41	26	55	15	F		0.57
0	3	154	38	3	48	4	F		-0.06
0	4	149	37	4	97	8	M		0.70
0	5	179	43	0	102	5	F		0.43
0	Mean	160	40	7	73	7.2			0.45
1.5	1	139	40	2	53	14	F	75	0.16
1.5	2	177	54	12	72	8	F	43	0.59
1.5	3	147	46	3	100	5	F	96	0.26
1.5	4	119	37	0	30	19	M	50	0.25
1.5	5	158	45	12	99	8	M	42	1.04
1.5	Mean	148	44	6	71	10.8		61	0.46
6.2	1	170	42	32	98	4	F	74	0.46
6.2	2	145	48	2	86	9	F	43	1.05
6.2	3	164	41	0	49	6	F	95	0.17
6.2	4	142	40	19	113	13	M	50	0.35
6.2	5	136	39	4	51	13	F	39	0.43
6.2	Mean	152	42	11	79	9.0		60	0.49
25	1	134	39	10	49	10	F	72	0.81
25	2	160	37	13	59	12	F	42	0.37
25	3	154	36	18	63	6	F	93	0.44
25	4	152	36	17	88	7	M	49	0.33
25	5	147	36	5	76	9	F	33	1.17
25	Mean	149	37	13	67	8.8		58	0.62
100	1	154	43	4	52	3	F	69	1.54
100	2	150	39	2	63	8	F	43	1.26
100	3	171	38	1	62	5	F	89	1.48
100	4	111	36	0	73	13	M	47	1.54
100	5	139	43	2	46	8	F	32	1.04
100	Mean	145	40	2	59	7.4		56	1.37
	MEAN	150.8	40.5	7.8	69.9	8.6		58.8	0.68

1.6 Plant Parts Experiment

Trmt	Rep	Hgt	Node	Buds	Flow	D>20	Sex	RH	1SRR
Con	1	153	43	70	1	7	F		0.64
Con	2	157	44	189	5	7	F		0.53
Con	3	162	40	64	3	5	F		0.44
Con	4	178	45	184	12	5	F		0.64
Con	5	140	43	66	18	11	F		0.52
Con	Mean	158	43	115	8	7			0.56
Top	1	138	40	92	8	3	M	49	0.65
Top	2	129	38	55	8	5	M	96	0.61
Top	3	168	46	95	3	4	F	96	0.60
Top	4	160	51	85	6	10	M	64	0.59
Top	5	161	41	64	9	4	M	54	0.54
Top	Mean	151	43	78	7	5		72	0.60
Mid	1	167	43	114	0	7	M	49	0.80
Mid	2	113	38	34	12	3	M?	96	0.26
Mid	3	165	39	92	9	6	F	97	0.16
Mid	4	150	43	87	11	7	M	64	0.89
Mid	5	140	45	27	1	13	?	54	1.30
Mid	Mean	147	42	71	7	7		72	0.68
Low	1	159	39	128	0	3	M	49	1.67
Low	2	159	49	78	9	8	F	96	0.61
Low	3	147	36	76	8	6	M	98	1.15
Low	4	147	44	60	7	5	F	64	0.62
Low	5	138	37	70	13	2	M	54	1.97
Low	Mean	150	41	82	7	5		72	1.20
Ax	1	153	34	78	4	6	M	49	0.66
Ax	2	122	40	93	5	7	F	97	0.60
Ax	3	149	44	78	6	3	F	98	0.59
Ax	4	139	43	47	2	5	M	65	0.36
Ax	5	138	41	60	6	3	F	53	0.43
Ax	Mean	140	40	71	5	5		72	0.53

cont'd...

1.6 (cont'd)

Trmt	Rep	Hgt	Node	Buds	Flow	D>20	Sex	RH	1SRR
Stem	1	165	40	87	8	7	F	52	0.55
Stem	2	172	42	89	7	10	F	97	0.60
Stem	3	106	41	25	2	8	M?	64	1.62
Stem	4	148	39	53	5	12	F	69	0.73
Stem	5	144	42	78	6	5	F	53	0.66
Stem	Mean	147	41	66	6	8		67	0.83
Bud	1	140	32	80	5	6	M	53	0.58
Bud	2	159	43	84	5	6	M	97	0.53
Bud	3	153	48	97	20	3	F	63	0.64
Bud	4	129	32	53	7	9	M	69	0.40
Bud	5	161	43	96	7	6	M	54	0.41
Bud	Mean	148	40	82	9	6		67	0.51
Side	1	139	34	51	2	4	?	56	1.22
Side	2	153	44	99	1	8	M	98	0.70
Side	3	138	34	78	18	3	F	63	0.84
Side	4	144	39	50	3	6	M?	70	0.51
Side	5	166	42	53	3	5	F	54	0.42
Side	Mean	148	39	66	5	5		68	0.74
All	1	152	37	83	6	6	?	58	0.39
All	2	141	36	72	2	5	M	98	0.99
All	3	146	37	58	6	2	F	62	0.26
All	4	148	42	59	6	3	F?	71	1.67
All	5	133	44	53	5	12	?	56	1.04
All	Mean	144	39	65	5	6		69	0.87
	MEAN	148.2	40.8	77.4	6.4	6.1		70.0	0.72

NB: con = untreated control; top, mid and low = top, middle and lower thirds of mother stem treated respectively; ax = treatment of axillary growth; stem, bud, side, all: parts of mother stem treated.

1.7 Leaf Side Experiment

Trmt	Rep	Hgt	Node	Buds	Flow	D>20	Sex	RH	1SRR
Con	1	144	32	55	0	5	M		0.57
Con	2	134	44	122	1	11	M		0.47
Con	3	142	40	112	0	11	M		0.45
Con	4	128	32	106	8	2	F		0.87
Con	5	146	41	117	2	5	F		0.58
Con	Mean	139	38	102	2	7			0.59
Up	1	128	31	86	0	6	M	73	0.57
Up	2	125	38	79	6	6	?	80	0.44
Up	3	132	46	47	0	4	?	78	0.24
Up	4	176	37	133	23	6	F?	98	1.21
Up	5	152	36	52	5	2	M	38	0.56
Up	Mean	143	38	79	7	5		73	0.60
Low	1	122	41	96	0	4	F	73	0.48
Low	2	140	37	100	4	1	?	83	0.89
Low	3	168	41	109	0	7	F	78	0.71
Low	4	151	39	84	11	11	F	100	0.40
Low	5	141	32	121	2	5	M	38	0.67
Low	Mean	144	38	102	3	6		74	0.63
	MEAN	141.9	37.8	94.6	4.1	5.7		73.9	0.61

NB: con = untreated control; up and low = upper and lower leaf surfaces respectively treated.

APPENDIX 2

Measurements of plants when harvested. Dose = dosage in mg ai glyphosate/plant; Trmt = treatment; Hgt = height of mother stem; D>20 = number of daughter stems exceeding 20 cm in height; DSF = number of daughter stems that flowered; tRDW = total dry weight (g) of regrowth produced in the 3 weeks following the main harvest; mRDW = mean dry weight (mg) of regrowth shoots; DM% = dry matter percentage of the stems cut at the main harvest; RtDW = root dry weight (g); lSRR = log shoot:root ratio.

2.1 Growth Stage Experiment - Vegetative Treatment

Dose	Rep	Hgt	D>20	DSF	tRDW	mRDW	DM%	RtDW	1SRR
0	1	139	21	7	0.45	150	61.5	7.9	1.36
0	2	147	11	0	5.2	226	13.9	44.0	0.64
0	3	174	10	5	4.9	213	44.6	24.9	1.11
0	4	99	14	1	10.0	417	19.7	66.4	0.43
0	5	127	9	5	5.2	193	25.3	52.3	0.77
0	Mean	137	13.0	3.6	5.1	240	33.0	39.1	0.86
1.5	1	68	18	9	8.1	202	20.1	61.9	0.68
1.5	2	72	16	4	7.1	182	26.9	71.8	0.57
1.5	3	45	11	2	5.8	171	22.6	90.8	0.29
1.5	4	90	6	2	2.9	223	18.5	26.3	0.74
1.5	5	56	10	3	7.5	167	26.8	55.4	0.60
1.5	Mean	66	12.2	4.0	6.3	189	23.0	61.2	0.58
6.2	1	39	14	0	7.0	184	15.2	20.3	0.62
6.2	2	78	15	4	14.9	216	23.9	57.3	0.67
6.2	3	68	6	2	4.6	242	18.5	21.3	0.78
6.2	4	60	5	4	7.3	365	21.0	52.9	0.57
6.2	5	47	7	3	7.0	368	26.1	67.9	0.55
6.2	Mean	58	9.4	2.6	8.2	275	20.9	43.9	0.64
25	1	47	5	0	12.4	776	15.7	33.2	0.40
25	2	59	6	0	7.9	304	23.3	36.0	0.63
25	3	35	13	0	0	0	69.0	4.6	1.22
25	4	37	5	0	1.9	95	49.4	7.2	0.72
25	5	66	14	0	8.4	233	14.6	33.5	0.46
25	Mean	53	8.2	0	6.1	352	34.4	22.9	0.68
100	1	49	20	0	6.2	144	22.1	37.0	0.35
100	2	70	12	0	7.7	148	30.6	13.0	0.76
100	3	70	7	0	0	0	66.9	0.7	1.86
100	4	46	2	0	0	0	62.4	0.2	2.20
100	5	59	10	0	1.6	109	32.0	27.6	0.18
100	Mean	59	10.2	0	3.1	134	42.8	15.7	1.07
	MEAN	74.7	10.6	3.4	5.77	242	30.8	36.6	0.77

2.2 Growth Stage Experiment - Early Bud Treatment

Dose	Rep	Hgt	D>20	DSF	tRDW	mRDW	DM%	RtDW	lSRR
0	1	137	7	7	3.7	308	36.1	61.0	0.80
0	2	149	9	9	3.6	300	24.6	34.5	0.88
0	3	154	11	6	4.4	275	19.3	39.1	0.87
0	4	147	11	2	4.6	354	20.5	58.2	0.71
0	5	177	8	5	1.9	173	29.0	29.7	0.90
0	Mean	153	9.2	5.8	3.6	262	25.9	44.5	0.83
1.5	1	113	8	3	3.1	195	22.2	41.7	0.67
1.5	2	99	10	7	5.6	280	26.4	37.3	0.86
1.5	3	113	11	2	4.4	220	2 .4	29.5	0.67
1.5	4	134	9	5	7.1	197	24.1	48.7	0.71
1.5	5	118	5	4	2.1	191	21.5	34.7	0.59
1.5	Mean	115	8.6	4.2	4.5	217	23.3	38.4	0.70
6.2	1	110	11	7	5.9	170	22.9	103.4	0.37
6.2	2	75	7	3	0.23	114	50.0	19.7	0.87
6.2	3	111	14	8	3.4	103	20.1	35.8	0.71
6.2	4	108	8	1	1.9	136	15.8	11.5	0.92
6.2	5	137	12	5	4.7	138	23.5	68.4	0.51
6.2	Mean	108	10.4	4.8	3.2	132	26.5	47.8	0.68
25	1	99	13	5	6.7	181	29.4	57.9	0.42
25	2	100	7	1	3.2	267	20.0	11.7	0.76
25	3	102	7	2	6.4	131	18.2	31.6	0.45
25	4	148	11	4	2.7	270	27.3	20.6	1.02
25	5	108	9	3	2.0	200	21.6	23.2	0.83
25	Mean	111	9.4	3.0	4.2	210	23.3	29.0	0.70
100	1	110	5	1	6.1	218	29.6	38.7	0.64
100	2	105	10	3	6.0	194	30.4	54.0	0.54
100	3	121	13	5	5.5	172	27.6	46.1	0.77
100	4	129	6	3	1.0	144	31.7	39.1	0.31
100	5	114	10	3	3.1	124	25.6	123.3	0.16
100	Mean	116	8.8	3.0	4.3	170	29.0	60.2	0.48
	MEAN	120.7	9.3	4.2	3.98	198	25.6	44.0	0.68

2.3 Growth Stage Experiment - Late Bud Treatment

Dose	Rep	Hgt	D>20	DSF	tRDW	mRDW	DM%	RtDW	1SRR
0	1	159	11	2	1.49	74	33.3	129.6	0.28
0	2	154	13	3	1.74	102	35.6	104.2	0.44
0	3	160	7	2	2.41	150	24.3	105.5	0.20
0	4	180	9	5	0.31	44	34.0	61.6	0.68
0	5	140	12	2	0.81	80	26.3	45.4	0.62
0	Mean	159	10.4	2.8	1.35	90.2	30.7	89.3	0.44
1.5	1	138	12	3	0.85	71	68.0	19.5	1.05
1.5	2	151	16	7	0.70	44	39.7	160.9	0.34
1.5	3	131	15	2	3.54	67	26.8	44.8	0.42
1.5	4	153	5	3	2.00	125	33.0	51.3	0.59
1.5	5	162	7	5	0	0	40.7	25.3	0.62
1.5	Mean	147	11.0	4.0	1.42	76.6	41.7	60.4	0.60
6.2	1	154	9	2	1.30	48	38.5	72.8	0.40
6.2	2	173	2	2	0.12	59	39.6	120.0	0.27
6.2	3	120	5	1	2.04	113	25.4	24.2	0.67
6.2	4	188	17	6	1.08	52	28.3	115.8	0.44
6.2	5	144	10	3	0	0	82.2	4.1	1.45
6.2	Mean	156	8.6	2.8	0.91	68.0	42.8	67.4	0.65
25	1	148	7	3	2.91	153	29.5	57.9	0.54
25	2	118	11	2	1.89	105	46.4	71.8	0.32
25	3	156	3	1	0	0	52.7	54.2	0.23
25	4	177	13	4	0.32	39	37.1	92.2	0.49
25	5	164	30	6	2.30	62	39.5	279.2	0.20
25	Mean	153	12.8	3.2	1.48	89.8	41.0	111.1	0.36
100	1	116	5	0	1.63	117	79.2	12.8	0.84
100	2	143	4	2	0	0	83.9	3.1	1.64
100	3	137	3	3	0.26	52	49.5	19.6	0.71
100	4	150	9	2	1.57	78	67.6	14.6	1.10
100	5	168	10	2	1.98	152	41.7	66.2	0.41
100	Mean	143	6.2	1.8	1.09	99.8	64.4	23.3	0.94
	MEAN	151.4	9.8	2.9	1.25	85.1	44.1	70.3	0.60

2.4 Growth Stage Experiment - Flowering Treatment

Dose	Rep	Hgt	D>20	DSF	tRDW	mRDW	DM%	RtDW	1SRR
0	1	167	23	8	1.77	93	29.9	156.8	0.39
0	2	101	8	3	1.34	96	25.2	54.1	0.36
0	3	150	7	4	1.26	181	32.8	208.4	0.17
0	4	133	6	5	0.43	86	36.6	84.8	0.55
0	5	128	9	6	0	0	41.8	227.6	0.10
0	Mean	136	10.6	5.2	0.96	91.1	33.3	146.3	0.31
1.5	1	143	12	5	1.17	78	26.7	146.4	0.10
1.5	2	155	10	7	1.53	109	28.6	83.9	0.46
1.5	3	133	12	7	2.07	99	40.8	116.3	0.37
1.5	4	155	7	3	0.94	187	51.8	44.2	0.67
1.5	5	159	10	6	0.05	8	41.1	78.8	0.48
1.5	Mean	149	10.2	5.6	1.15	96.1	37.8	93.9	0.42
6.2	1	132	8	6	0.66	44	46.2	146.8	0.07
6.2	2	116	17	7	2.03	119	37.2	57.4	0.49
6.2	3	158	20	9	1.42	75	34.4	102.7	0.45
6.2	4	130	10	2	0.73	37	50.8	26.7	0.79
6.2	5	104	16	4	0.50	28	53.1	59.1	0.41
6.2	Mean	128	14.2	5.6	1.07	60.6	44.3	78.5	0.44
25	1	142	8	3	3.20	80	30.8	97.0	0.26
25	2	145	10	7	0.32	53	39.1	168.9	0.42
25	3	122	10	2	1.59	84	61.2	37.5	0.60
25	4	153	8	3	2.09	174	61.1	81.9	0.29
25	5	136	14	5	0.76	69	69.4	34.8	0.98
25	Mean	140	10.0	4.0	1.59	92.0	52.3	84.0	0.51
100	1	166	10	6	0.69	115	41.3	61.3	0.72
100	2	145	6	2	0.01	8	54.4	48.2	0.50
100	3	174	4	2	0	0	85.8	11.5	1.13
100	4	168	10	2	0	0	82.2	0.8	2.41
100	5	154	10	5	0.11	7	74.5	73.7	0.55
100	Mean	161	8.0	3.4	0.16	43.4	67.6	39.1	1.06
	MEAN	142.8	10.6	4.8	0.99	79.5	47.1	88.4	0.55

2.5 Growth Stage Experiment - Post-flowering Treatment

Dose	Rep	Hgt	D>20	DSF	tRDW	mRDW	DM%	RtDW	lSRR
0	1	156	11	4	0.12	12.2	38.3	79.9	0.61
0	2	165	21	7	1.10	73.1	75.5	125.9	0.57
0	3	154	12	2	0	0	56.4	253.9	-0.06
0	4	149	10	7	0.51	56.2	56.2	64.9	0.70
0	5	179	9	5	0.01	3.2	46.5	158.9	0.43
0	Mean	161	12.9	5.0	0.35	36.2	54.6	136.7	0.45
1.5	1	139	19	12	0.11	16.4	45.1	224.7	0.16
1.5	2	177	10	5	0.09	18.6	60.2	110.4	0.59
1.5	3	147	5	3	0.01	7.0	47.9	114.2	0.26
1.5	4	121	27	9	0.07	8.1	34.9	135.3	0.25
1.5	5	158	8	2	0	0	86.5	17.0	1.04
1.5	Mean	148	13.8	6.2	0.058	12.5	54.9	120.3	0.46
6.2	1	170	4	4	0	0	39.3	128.1	0.46
6.2	2	145	9	5	0.15	24.8	67.9	16.4	1.05
6.2	3	166	6	5	0	0	48.0	153.1	0.17
6.2	4	143	16	12	0.04	36.0	64.2	152.8	0.35
6.2	5	136	14	13	0.002	2.0	72.5	123.0	0.43
6.2	Mean	152	9.8	7.8	0.037	20.9	58.4	114.7	0.49
25	1	134	11	8	0.63	69.9	65.2	30.4	0.81
25	2	160	17	6	0.53	47.9	63.4	159.2	0.37
25	3	154	6	3	0.30	101.3	41.2	109.4	0.44
25	4	152	8	6	0.10	11.1	66.6	151.5	0.33
25	5	147	11	7	0.36	27.6	81.1	28.4	1.17
25	Mean	149	10.6	6.0	0.38	51.6	63.5	95.8	0.62
100	1	154	3	1	0	0	82.5	2.8	1.54
100	2	150	8	6	0	0	82.5	9.3	1.26
100	3	171	5	4	0.04	10.0	87.6	5.9	1.48
100	4	112	17	12	0.06	5.2	67.0	6.4	1.54
100	5	139	8	6	0.01	4.0	81.8	23.7	1.04
100	Mean	145	8.2	5.8	0.021	6.4	80.3	9.6	1.37
	MEAN	151.1	11.0	6.2	0.169	28.1	42.0	95.4	0.68

2.6 Plant Parts Experiment

Trmt	Rep	Hgt	D>20	DSF	tRDW	mRDW	DM%	RtDW	lSRR
Con	1	158	17	11	2.1	150	26.1	92.0	0.64
Con	2	157	15	8	3.7	185	29.5	134.3	0.53
Con	3	162	13	3	4.12	179	25.2	102.4	0.44
Con	4	178	14	4	0.87	72	33.2	65.9	0.64
Con	5	144	17	8	2.16	103	23.3	102.6	0.52
Con	Mean	160	15.2	6.8	2.59	138	27.5	99.4	0.56
Top	1	138	12	2	0.57	71	26.5	23.5	0.65
Top	2	129	7	3	0.64	71	26.3	45.9	0.61
Top	3	168	4	4	0.91	114	37.4	67.1	0.60
Top	4	160	14	6	0.24	35	34.1	54.1	0.59
Top	5	161	7	2	1.83	61	48.8	49.2	0.54
Top	Mean	151	8.8	3.4	0.84	70	34.6	48.0	0.60
Mid	1	173	8	5	1.61	201	28.5	44.0	0.80
Mid	2	113	3	1	1.27	106	25.2	43.5	0.26
Mid	3	165	6	5	3.04	113	23.9	80.2	0.16
Mid	4	150	24	2	2.11	75	36.2	20.0	0.89
Mid	5	140	13	1	0	0	80.2	6.7	1.30
Mid	Mean	148	10.8	2.8	1.61	99	38.8	38.9	0.68
Low	1	162	4	1	0	0	81.6	2.3	1.67
Low	2	159	8	2	1.51	101	42.4	40.4	0.61
Low	3	147	7	3	0	0	79.2	9.3	1.15
Low	4	156	5	2	3.10	221	45.8	48.4	0.62
Low	5	138	2	2	0	0	81.8	1.1	1.97
Low	Mean	152	5.2	2.0	0.92	64	66.2	20.4	1.20
Ax	1	153	6	5	4.7	362	30.6	58.0	0.66
Ax	2	123	15	6	4.2	131	20.6	45.3	0.60
Ax	3	149	3	0	2.05	146	23.9	24.3	0.59
Ax	4	142	7	3	2.51	279	29.2	83.6	0.36
Ax	5	138	4	1	1.27	159	26.2	50.8	0.43
Ax	Mean	141	7.0	3.0	2.95	215	26.1	52.4	0.53

cont'd...

2.6 (cont'd)

Trmt	Rep	Hgt	D>20	DSF	tRDW	mRDW	DM%	RtDW	lSRR
Stem	1	165	11	7	3.5	97	37.4	55.1	0.55
Stem	2	174	10	5	2.62	125	35.4	94.3	0.60
Stem	3	106	10	1	0	0	79.8	1.9	1.62
Stem	4	148	13	3	1.50	83	42.8	38.8	0.73
Stem	5	144	7	4	2.41	172	34.6	45.1	0.66
Stem	Mean	147	10.2	4.0	2.01	95	46.0	47.0	0.83
Bud	1	140	15	7	2.6	79	30.9	79.9	0.58
Bud	2	159	8	6	2.3	164	32.6	80.6	0.53
Bud	3	154	3	2	0.14	68	36.7	45.2	0.64
Bud	4	129	12	6	2.73	88	34.0	82.4	0.40
Bud	5	161	8	7	1.23	136	33.7	113.6	0.41
Bud	Mean	149	9.2	5.6	1.80	107	33.6	80.3	0.51
Side	1	139	9	2	1.06	75	40.6	7.0	1.22
Side	2	155	11	4	2.75	211	30.2	51.0	0.70
Side	3	139	10	2	0.83	207	51.8	24.5	0.84
Side	4	144	12	1	2.72	124	51.1	39.1	0.51
Side	5	166	5	5	0.03	6	30.3	98.8	0.42
Side	Mean	149	9.4	2.8	1.48	125	40.8	44.1	0.74
All	1	152	8	0	4.2	124	24.6	62.0	0.39
All	2	141	6	2	1.71	190	30.8	15.3	0.99
All	3	146	5	2	0.69	43	29.7	49.5	0.26
All	4	148	3	0	0	0	80.5	1.8	1.67
All	5	133	14	0	0.42	60	78.0	18.6	1.04
All	Mean	144	7.2	0.8	1.41	83	48.7	29.4	0.87
	MEAN	149.0	9.2	3.5	1.73	110.9	40.2	51.1	0.72

NB: con = untreated control; top, mid and low = top, middle and lower thirds of the mother stem treated respectively; ax = treatment of axillary growth; stem, bud, side, all = parts of mother stem treated.

2.7 Leaf Side Experiment

Trmt	Rep	Hgt	D>20	DSF	tRDW	mRDW	DM%	RtDW	lSRR
Con	1	148	10	5	3.0	333	33.8	78.6	0.57
Con	2	138	22	10	4.8	130	23.8	94.0	0.47
Con	3	150	18	12	1.4	87	31.1	128.5	0.45
Con	4	128	5	3	2.0	167	24.6	31.0	0.87
Con	5	147	8	5	4.9	258	24.5	66.2	0.58
Con	Mean	142	12.6	7.0	3.22	195	27.6	79.7	0.59
Up	1	138	8	5	7.1	296	31.3	59.1	0.57
Up	2	125	9	0	2.5	139	19.8	39.8	0.44
Up	3	136	5	0	2.9	193	22.3	49.6	0.24
Up	4	176	7	3	0	0	83.5	9.7	1.21
Up	5	152	4	2	3.5	206	23.4	36.9	0.56
Up	Mean	145	6.6	2.0	3.20	208	36.1	39.0	0.60
Low	1	134	5	2	4.0	333	22.4	42.7	0.48
Low	2	144	1	0	3.3	150	77.8	11.8	0.89
Low	3	170	8	3	4.2	89	39.7	42.0	0.71
Low	4	152	13	5	5.7	178	28.9	93.4	0.40
Low	5	144	7	1	0.02	21	44.2	31.4	0.67
Low	Mean	149	6.8	2.2	3.44	154	42.6	44.3	0.63
	MEAN	145.5	8.7	3.7	3.28	184	35.4	54.3	0.61

NB: con = untreated control; up and low = upper and lower leaf surfaces treated respectively.

APPENDIX 3

Analyses of variance for data cited in the text.

df = degrees of freedom; MS = mean square;

CV = coefficient of variation; SE = standard error.

Significance: NS not significant

* 0.05 > P > 0.01

** P < 0.01

3.1 Stem dry matter percentage of all plants in the Growth Stage Experiment.

Source	df	MS	F	Sig
Dose	4	1929	10.1	**
Stage	4	5237	27.4	**
Dose x Stage	16	186	1.0	NS
Residual	100	191		
Total	124	410		
CV = 33.0%		SE = 13.8		

3.2 Stem matter percentages of untreated controls from all experiments.

Source	df	MS	F	Sig
Stage	6	484.8	4.65	**
Residual	28	104.2		
Total	34	171.4		
CV = 30.7%		SE = 10.2		

3.3 Total regrowth dry weight produced by untreated controls from all experiments.

Source	df	MS	F	Sig
Stage	6	14.31	5.49	**
Residual	28	2.61		
Total	34	4.67		
CV = 65.5%		SE = 1.61		

3.4 Number of regrowth shoots produced by plants in the Growth Stage Experiment.

Source	df	MS	F	Sig
Dose	4	176.3	1.27	NS
Stage	4	1592.3	11.46	**
Dose x Stage	16	110.2	0.79	NS
Residual	100	139.0		
Total	124	183.4		
CV = 74.3%		SE = 11.8		

3.5 Mean individual size of regrowth shoots produced by plants in the Growth Stage Experiment.

Source	df	MS	F	Sig
Dose	4	20955	3.35	*
Stage	4	180951	28.90	**
Dose x Stage	16	8207	1.31	NS
Residual	100	6262		
Total	124	12622		
CV = 68.5%		SE = 79.1		

3.6 Total regrowth dry weight produced by plants in the Growth Stage Experiment.

3.6.1 Table of means.

Dose (mg/plant)	0	1.5	6.2	25	100
DW (g)	2.29	2.67	2.68	2.76	1.74

3.6.2 Analysis of variance.

Source	df	MS	F	Sig
Dose	4	4.49	1.14	NS
Stage	4	138.11	34.99	**
Dose x Stage	16	3.90	0.99	NS
Residual	100	3.95		
Total	124	8.29		
CV = 81.8%		SE = 1.99		

3.7 Log shoot:root ratio of untreated controls from all experiments.

Source	df	MS	F	Sig
Stage	6	0.2073	4.18	**
Residual	28	0.0496		
Total	34	0.0774		
CV = 38.5%		SE = 0.223		

3.8 Log shoot dry weight of untreated controls from all experiments.

Source	df	MS	F	Sig
Stage	6	0.0269	1.87	NS
Residual	28	0.0144		
Total	34	0.0166		
CV = 4.9%		SE = 0.120		

3.9 Log root dry weight of untreated controls from all experiments.

Source	df	MS	F	Sig
Stage	6	0.263	4.78	**
Residual	28	0.055		
Total	34	0.092		
CV = 12.5%		SE = 0.234		

3.10 Log shoot:root ratio of plants in the Plant Parts Experiment.

Source	df	MS	F	Sig
Part	8	0.246	1.77	NS
Residual	36	0.139		
Total	44	0.159		
CV = 51.5 %		SE = 0.37		

3.11 Log shoot:root ratio of plants in the Leaf Side Experiment.

Source	df	MS	F	Sig
Treatment	2	0.00245	0.038	NS
Residual	12	0.06530		
Total	14	0.05632		
CV = 42.1%		SE = 0.25		

3.12 Root dry weight of plants in the Plant Parts Experiment.

Source	df	MS	F	Sig
Part	8	3023	4.43	**
Residual	36	682		
Total	44	1108		
CV = 51.1%		SE = 26.11		

3.13 Root dry weight of plants in the Leaf Side Experiment.

Source	df	MS	F	Sig
Treatment	2	2443	2.88	NS
Residual	12	847		
Total	14	1075		
CV = 53.6%		SE = 29.1		

3.14 Log shoot:root ratio of plants in the Growth Stage Experiment.

Source	df	MS	F	Sig
Dose	4	4.680	6.78	**
Stage	4	0.846	1.22	NS
Dose x Stage	16	1.188	1.72	NS
Residual	100	0.691		
Total	124	0.889		
CV = 55.4%		SE = 0.831		

3.15 Log shoot:root ratio of plants treated with 100 mg in the Growth Stage Experiment.

Source	df	MS	F	Sig
Stage	4	0.525	1.47	NS
Residual	20	0.357		
Total	24	0.385		
CV = 60.6%		SE = 0.598		

3.16 Shoot dry weight of plants in the Leaf Side Experiment.

Source	df	MS	F	Sig
Treatment	2	28716	9.82	**
Residual	12	2925		
Total	14	6609		
CV = 28.1%		SE = 54.1		

APPENDIX 4

Correlation coefficients (r) between the log shoot:root ratio and the factors listed for plants treated at the vegetative stage with 6.2, 25 and 100 mg of glyphosate.

Factor	r	Sig.
% of nodes on mother stem with axillary growth when treated	-0.63	*
Height of mother stem when treated	-0.04	NS

Significance: NS not significant
* $0.05 > P > 0.01$

APPENDIX 5

Chi-square analysis of male:female ratio.

Number of males = 115

Number of females = 140

$$X^2 = \sum \frac{(|Ob - Ex| - 0.5)^2}{Ex}$$

$$= \frac{(|140 - 127.5| - 0.5)^2}{127.5} + \frac{(|115 - 127.5| - 0.5)^2}{127.5}$$

$$= 2.259$$

Not significant at 10% level of probability.

NB: Ob = observed value

Ex = expected value

Yates correction for continuity was used.